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Washington, D. C. ▼ March, 1927

VARIABILITY IN THE LINKAGE OF TWO SEED CHARACTERS OF MAIZE

By

G. N. COLLINS, Senior Botanist in Charge, and
J. H. KEMPTON, Associate Botanist, Biophysical Laboratory
Bureau of Plant Industry

July 1872

CONTENTS

	Page
Introduction	1
Statistical Treatment	4
Variability of Crossover Rate	8
Rate of Crossing Over between the C–Wx Genes	24
Correlations	56
Discussion	60
Summary	62
Literature Cited	64

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By G. N. Collins, *Senior Botanist in Charge*, and J. H. Kempton, *Associate Botanist, Biophysical Laboratory, Bureau of Plant Industry*

CONTENTS.

	Page
Introduction	1
Statistical treatment	4
Variability of crossover rate	8
Variability not unique in C–Wx linkage nor in Chinese-Algeria maize hybrids	8
Crossover rate more variable in some progenies than in others	10
Variability of crossing over no greater in male than in female gametes	13
Variability of crossing over no greater in upper than in lower ears	15
Variability of crossing over no greater in the base than in the tip of the ear	15
Crossing over generally less variable in several samples of the same individual than in single samples from several individuals	16
Crossing over less variable in samples from different parts of the same male inflorescence than in samples from several inflorescences	18
Variability of crossing over no greater in old than in fresh pollen	19
Crossing over no more variable in first than in last gametes formed	19
Crossover ratio more variable than Mendelian ratios	20
Variability in the crossover class not the result of differential death rate of zygotes	21
Variability of crossover rate—Contd.	
Variability of rate of crossing over alike in plants heterozygous and homozygous dominant for R	23
Rate of crossing over between the C–Wx genes	24
Crossing over greater in some progenies than in others	25
Proportion of crossover to noncrossover gametes not affected by vitality of pollen	27
Crossing over reduced by the R aleurone factor in a heterozygous condition	31
Rate of crossing over between C and Wx associated with the Su factor	35
Rate of crossing over differs in the two sexes	36
Rate of crossing over not alike in the upper and lower ears of the same plant	45
Rate of crossing over not alike in base and tip of the same ear	49
Length of silk not a factor in rate of crossing over	52
Variations in meteorological conditions during anthesis not a factor in rate of crossing over	53
Rate of crossing over similar in first and last pollen shed	55
Correlations	56
Discussion	60
Summary	62
Literature cited	64

INTRODUCTION

The improvement of plants and animals by systems of breeding is contingent upon the inheritance of the qualities it is desired to perpetuate. In consequence, much emphasis of late has been placed upon an understanding of the fundamental principles underlying

the transmission of characters, in an effort to remove some of the uncertainties of breeding and to provide a basis for a more orderly procedure for future improvement.

The manner in which new characters arise is still in dispute, but with the progress of investigation it has become increasingly clear that the process of the transmission of characters is largely mechanical. For purposes of convenience the characters manifested to our perceptions are thought of as resulting from the interaction of genes, invisible determiners located in the germ cells. These hereditary elements are transmitted from one generation to another ordinarily without change. Some characters are relatively simple, requiring for expression but a single gene, but all degrees of complexity exist, some of which exceed the limits of our present ability to analyze the hereditary constituents into their component parts.

The genes occur in groups; groups which in some organisms correspond to the haploid number of chromosomes, leading to the belief that the chromosomes are packages of genes.

Experimental evidence of exceptional accuracy has been acquired from many sources showing that the genes are arranged in a linear series with respect to one another and always in the same order.

Further, it has been possible to measure the distance separating the genes in any given group, not in actual units of linear measure but relatively to one another. The distance between related genes expresses their correlation and measures the extent to which they will appear together in inheritance. Genes which appear together in inheritance are spoken of as linked and the phenomenon is known as linkage.

To study linkage relations the procedure is to cross two individuals that differ with respect to two characters, the genes of which are located in the same chromosome. In the first generation the dominant form of both characters is expressed. The first-generation individuals will produce gametes of four kinds representing the four possible combinations as follows: (1) Both characters like the female parent; (2) both characters like the male parent; (3) one character like the female parent, the other character like the male parent; (4) like 3 with the characters reversed. The nonparental combinations, 3 and 4, are called the crossover class. The percentage of the total number of gametes that falls into this class is the percentage or rate of crossing over.

If the second generation is the result of back crossing the first-generation individuals with individuals homozygous recessive for both of the characters, the characters of each effective gamete produced by the hybrid individual will be expressed in the offspring. If the two characters are completely independent, the four combinations will occur in equal numbers and the two combinations representing the crossover class will be 50 per cent of the total. If crossing-over percentages in excess of 50 were found they would represent disherences, or cases where the characters descended from opposite parents tend to become associated in inheritance.

With the demonstration of the linear arrangement of genes separated by measurable distances, the question has arisen as to the stability of these distances. This question of stability is of more than theoretical interest, since plant improvement through breeding often depends upon the facility with which character combinations can be

dissolved or upon the certainty with which a given complex of linked characters can be relied upon to remain in combination.

Geneticists working with Drosophila have demonstrated the existence of many factors both heritable and environmental that affect the degree of relationship of certain genes. The data accumulated by the several investigators who have considered the problem of variability in crossover rate have been assembled and evaluated by Morgan, Bridges, and Sturtevant (*13*).[1] For a thorough discussion of the genetic and environmental factors that affect crossing over in Drosophila the reader is referred to these authors.[2]

The nature of the mechanism assumed, to provide a means for the transfer of heritable elements from one chromosome to another, is such as to render any very definite rates of transfer extremely improbable yet genetic literature abounds in discussions that aim to fix within one or two units the distances that separate two genes.

Those working with characters of mature plans where populations are limited to hundreds of individuals long have recognized the futility of attempting to establish crossover rates other than to determine whether a given pair of genes is linked or independent. Where distances are approaching 50 units even this modest effort is not always successful, and in many cases investigators have succeeded only in amassing conflicting data which for definite interpretation must await the discovery of characters located at the intermediate positions.

With the seed characters of maize it is possible to go somewhat further, for with these characters large populations are matured under very uniform conditions, yet even here much variability is encountered.

Investigators of linkage phenomena in maize are familiar with the fact that in tests involving a number of ears some will be found that depart from the crossing-over mean of the progeny by percentages too large to be ascribed to chance. This is especially noticeable in linkages involving seed characters where relatively large populations are possible and the significance of the aberrant ratios can be established conclusively.

In numerous progenies involving the linked pair of factors *C* and *Wx*[3] individual ears have been found having as low as 8 per cent and as high as 50 per cent of crossing over. In these cases the individual ears clearly were aberrant as far as the percentage of crossing over was concerned, and the observed percentage could not be considered as due to errors of random sampling from a population having the percentage of crossover gametes indicated by the mean of the progeny in which they appeared.

The material used for the most part has arisen from a single cross between the Chinese waxy maize and a colored pop corn from Algeria. Numerous progenies have been grown from the original cross in the course of experiments attempting to interpret aberrant aleurone, waxy, or crossover ratios, and though most of these prob-

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[1] Italic numbers in parenthesis refer to "Literature cited," p. 64.

[2] Since this bulletin was prepared there has appeared a comprehensive study of crossover variability in maize by Stadler (*17*). Although many of the conclusions here presented are in accord with those of Stadler, in some instances there is disagreement. He also presents data on some features not considered in this paper. For a more complete understanding of the several points involved both papers should be consulted.

[3] *C* is a factor necessary to the production of aleurone color and *Wx* is the factor that differentiates horny and waxy endosperm.

lems remain unsolved the efforts have resulted in the accumulation of a large mass of data which can be utilized for an analysis of linkage.

The data available as to the linkage relations of these factors show that stability of crossover rates is no more to be expected than stability in other biologic processes. Almost any possible grouping of the data brings to light significant differences in the rate of crossing over, if the numbers involved are sufficiently large, and it is the purpose of the writers to consider some of these differences and their causes.

The rate of crossing over in the formation of gametes must be inferred from zygotic ratios, and observed changes may be due (1) to changes in the proportion of crossover gametes formed, (2) to a differential death rate of crossover gametes, (3) to selective fertilization, or (4) to a differential death rate of zygotes.

Strictly speaking, changes other than those specified in 1 are not changes in the rate of crossing over. Both 1 and 2 are gametic and there is little hope of being able to distinguish between them except through refinements of cytological methods.

It is not a simple matter to make even the general distinction between gametic and zygotic variation in the rate of crossing over. Selective fertilization as a source of variation is eliminated when the crossing over is measured by back crosses of which one parent has the gametes all of one kind in respect to the characters under consideration.

A differential death rate of zygotic classes may be detected by a comparison of linkage and repulsion values. But to do this the comparison must be made between distinct progenies, and the experiments show that sister progenies often differ significantly in crossing over.

Another method of detecting differential death rates of zygotic classes is to cross two individuals having the gametic compositions *A a b b* and *a a B b*. This will yield a population with all four classes and no opportunity for linkage. Here again individual diversity precludes the possibility of generalization. With progenies involving the same two characters there are some that show significant departures from equality of the four classes, while in closely related progenies no difference appears.

In view of the variability of the crossover ratio it was thought to be desirable to consider the factors that were associated with this instability before considering the conditions that bring about changes in the rate. Accordingly, in the present bulletin the data are first scrutinized from the standpoint of variability and then considered from the standpoint of the factors associated with changes in the rate.

STATISTICAL TREATMENT[4]

In dealing with variations and differences in the percentages of characters or of crossing over, the significance assigned to the results

[4] Explanation of Statistical Symbols.—N=number of subgroups, n=number of seeds, M=mean, M_p=mean percentage, PE=probable error, D/E=difference divided by the probable error, E_d=probable error of a difference, p=percentage, q=100 minus p, Q=Yule's coefficient of association, r=product moment coefficient of correlation, Σ=summation, σ=standard deviation, σ_1=standard deviation of x array, σ_2=standard deviation of y array, σ_{1-2}=standard deviation of $x-y$ array, σ_{50}=standard deviation corrected to 50 per cent, σ_{50p}=standard deviation corrected to 50 per cent and for size of population, H=harmonic mean, $\chi_1=0.67449/\sqrt{n}$.

(observed measures) depends upon the choice of a method for calculating the probable errors. Throughout the present bulletin the attempt is made to apply to the observed means and differences the method that would be most critical.

In general, three formulæ have been used in dealing with the probable errors of ratios.

For the probable error of percentages on individual ears use is made of the familiar formula

$$PE = \frac{0.67449}{\sqrt{n}}\sqrt{pq} \tag{1}$$

where n=the number of seeds, p=the percentage, and q=100 minus the percentage of the character concerned.

In this operation the calculations are greatly facilitated by the use of the tables of Miner (*12*) for the value of pq and of Pearson (*14*) for the values of $0.67449/\sqrt{n}$.

For the probable error of the mean percentage or rate of crossing over in a progeny or group of individuals this formula gives too small a value except in those cases where there is no individual diversity. If the crossover values of the individual ears are not chance departures from a common mean, the reliability of the general mean is influenced by the number of ears involved.

For these cases the observed percentages of the individual ears have been treated as an array for which the standard deviation was calculated. Since the ears vary in size, the squared departures from the mean were weighted by the number of seeds on the ear.

For the probable error of the mean percentage, use is made of the formula

$$PE = \frac{0.67449}{\sqrt{N}}\sigma = \frac{0.67449}{\sqrt{N}}\sqrt{\frac{\Sigma np^2}{\Sigma n} - M_{p2}} \tag{2}$$

where p=the percentage, n=the number of seeds, M_p=mean percentage, and N=the number of ears.

Where the problem involved differences between pairs of ears, still a third method was used. For these cases the differences between the paired ears were taken as an array for which the standard deviation was caluculated.

Since the differences were between ears of various sizes, it was essential to employ a weighting factor, but the differences may not be weighted by the number of seeds, because the ears of a pair vary in size. Thus a given difference based on two ears, one of 100 seeds and the other of 800, calculated by the mean number of seeds, would have the same weight as a difference between two ears each of 450 seeds, whereas the significance of the latter difference would be very much greater.

Accordingly, recourse is had to weighting the differences by the reciprocal of the square of the probable error of the difference where the errors of each ear were calculated by formula 1.

The formula for the probable error of a mean difference is

$$PE_d = \frac{0.67449}{\sqrt{N}}\sigma = \frac{0.67449}{\sqrt{N}}\sqrt{\Sigma d^2 \frac{1}{E_d^2}\Big/\Sigma\frac{1}{E_d^2} - M_d^2} \tag{3}$$

where d=difference, E_d=probable error of the difference, N=number of ears, and M_d=weighted mean difference= $\Sigma d\frac{1}{E_d^2}\Big/\Sigma\frac{1}{E_d^2}$.

In all populations of 20 or less, the standard deviation and probable errors of the mean have been increased by using the correction of Pearson (*15*) for the standard deviation of small numbers.

In applying this correction in the calculation of probable errors Table 1 was found a convenience. This table was prepared by dividing the values of $\chi_1=0.67449/\sqrt{n}$ of Pearson's tables by the constants given for the correction of small samples. In use, the observed standard deviation is multiplied by $\frac{\chi_1}{\Sigma/\sigma}$, the value opposite the number of individuals in the population.

TABLE 1.—*Factors for converting standard deviations* (σ) *of small populations into probable errors*

Number	$\frac{\chi_1}{\Sigma/\sigma}$	Number	$\frac{\chi_1}{\Sigma/\sigma}$	Number	$\frac{\chi_1}{\Sigma/\sigma}$
4	0.42266	10	0.23116	16	0.17707
5	.35880	11	.21868	17	.17128
6	.31702	12	.20805	18	.16602
7	.28702	13	.19880	19	.16120
8	.26417	14	.19069	20	.15679
9	.24601	15	.18351		

In comparing the variability of two or more populations it is customary to make use of the coefficient of variability. The coefficient of variability is the standard deviation expressed as a percentage of the mean. When direct physical measurements are involved the use of this constant is desirable, since it corrects for the change in standard deviation that follows a change in absolute magnitude of the measurements. The coefficient of variability is of doubtful value, however, when applied to ratios such as rate of crossing over or Mendelian percentages. In series of ratios there usually is a high negative correlation between the mean and the coefficient of variability which can mean only that the coefficient of variability is influenced unduly by the magnitude of the mean.[5] Examples of this relationship may be seen in Tables 3 and 5. On the other hand, it is in the nature of ratios to show a decreasing variability as the mean ratio departs from 0.5, or 50 per cent. This follows, of course, from the fact that the range of ratios is limited between 0 and 1.

The standard deviation of a ratio is $\sqrt{pq}$, where p=the number in one class divided by the total number and q=1−p. The standard deviation of a series of ratios each based on the same number, n, is $\sqrt{pq/n}$.

[5] Gowen (7) has calculated the coefficient of variability of the observed percentages of double crossing over in the third chromosome of Drosophila and concludes that the variability in double crossing over is markedly higher than in single crossing over. It would appear that the large coefficients in the double-crossover ratio are a direct consequence of the very low mean percentages. The observed standard deviations are actually smaller than in the single crossing over, but corrected to 50 per cent, the variability in the two groups is of the same order, as would be expected from the close relation existing between the two processes.

TABLE 2.—*Formulæ for deriving p from Q for a number of gametic combinations*[1]

Gametic combination	Zygotic ratio	Formula
$\frac{\widehat{A\ B}}{a\ b} \times \frac{a\ b}{a\ b}$	1:1	$p = \frac{Q-1+\sqrt{1-Q^2}}{2Q}$
$\frac{\widehat{A\ b}}{a\ B} \times \frac{a\ b}{a\ b}$	1:1	
$\frac{\widehat{A\ B}}{a\ b} \times \frac{\widehat{A\ B}}{a\ b}$	3:1	$p^2 = \frac{\sqrt{4-2Q(Q-1)}-2}{2Q}$
$\frac{\widehat{A\ b}}{a\ B} \times \frac{\widehat{A\ b}}{a\ B}$	3:1	
$\frac{\widehat{A\ B\ B'}}{a\ b\ b'} \times \frac{a\ b\ B'}{a\ b\ b'}$	1:1	$p = \frac{3Q-4+\sqrt{16-15Q^2}}{6Q}$
$\frac{\widehat{A\ b\ B'}}{a\ B\ b'} \times \frac{a\ b\ B'}{a\ b\ b'}$	1:1	
$\frac{\widehat{A\ B\ b'}}{a\ b\ B'} \times \frac{a\ b\ B'}{a\ b\ b'}$	1:1	
$\frac{\widehat{A\ B}}{a\ b} \times \frac{A\ b}{a\ b}$	3:1	$p = \frac{Q-2+\sqrt{4-3Q^2}}{2Q}$
$\frac{\widehat{A\ b}}{a\ B} \times \frac{A\ b}{a\ b}$	3:1	
$\frac{\widehat{A\ B\ B'}}{a\ b\ b'} \times \frac{a\ b\ b'}{a\ b\ b'}$	1:1	
$\frac{\widehat{A\ b\ B'}}{a\ B\ b'} \times \frac{a\ b\ b'}{a\ b\ b'}$	1:1	
$\frac{\widehat{A\ B\ B'}}{a\ b\ b'} \times \frac{\widehat{A\ B\ B'}}{a\ b\ b'}$	3:1	$p^2 = \frac{Q-8+\sqrt{64+8Q-47Q^2}}{6Q}$
$\frac{\widehat{A\ b\ B'}}{a\ B\ b'} \times \frac{\widehat{A\ b\ B'}}{a\ B\ b'}$	3:1	
$\frac{\widehat{A\ B\ B'}}{a\ b\ b'} \times \frac{A\ b\ b'}{a\ b\ b'}$	3:1	$p = \frac{Q-2+\sqrt{4-2Q-2Q^2}}{Q}$
$\frac{\widehat{A\ b\ B'}}{a\ B\ b'} \times \frac{A\ b\ b'}{a\ b\ b'}$	3:1	
$\frac{\widehat{A\ B\ b'}}{a\ b\ b'} \times \frac{a\ B\ b'}{a\ b\ b'}$	1:1	$p = \frac{Q-4+\sqrt{16-15Q^2}}{2Q}$
$\frac{\widehat{A\ b\ B'}}{a\ B\ b'} \times \frac{a\ B\ b'}{a\ b\ b'}$	1:1	

[1] A and B are the dominant allelomorphs of the factor pairs, $A\ a$, $B\ b$. A' and B' are the dominant allelomorphs of the pairs, $A'\ a'$, $B'\ b'$. The primed letters represent complementary genes. The curved line connecting the factor symbols indicates a linkage of those factors. p=the percentage of crossing over.

Since the fluctuations in ratios due to errors of sampling become smaller as the ratio departs from 0.5, and the change is measured by the change in $\sqrt{pq}$, it is possible to correct for these changes by multiplying the observed standard deviation by $0.5/\sqrt{pq}$. This changes the standard deviation to that expected had the mean ratio been 0.5, or 50 per cent. Standard deviations corrected by the factor $0.5/\sqrt{pq}$ are designated σ_{50}. This correction neglects the fact that for small ratios plus variations will be more frequent than minus variations,

but the error from this source is small. The formula for the difference between plus and minus variations is given by Haldane (*8*) as $0.3033(1-2p)/n$, to be added to the probable error in excess and subtracted from the probable error in defect.

For a discussion of the variability of percentages, see Wright (*18*).

To determine whether the variability in a series of observed ratios is greater than the expected in random samples from a single population, the observed standard deviation is compared with the standard deviation of the mean ratio, $\sqrt{pq/n}$. Where the number on which the individual ratios is based varies, Yule (*19*) has been followed and the harmonic mean of the numbers (H) taken for the value of n.

The formula for the expected standard deviation in a series of ratios (expressed as percentages), if the variations are due only to errors of sampling, is $\sqrt{pq/H}$, where p=the mean percentage, q=$100-p$, and $H=N\Big/\Sigma\frac{1}{n}$, n being the number on which the individual percentage is based and N the number of percentages in the series.

All linkage values have been calculated from the coefficient of association, Q. The merits and limitations of this method have been outlined by Collins (*5*). It was applied to the studies in hand and even to the back crosses, because by this method the crossover values are not distorted by differential death rates of zygotic classes, except in the event that the death rate of a combination of characters differs from the combined death rate of the single characters. The Bridges (*3*) method of balanced viability could not be used without introducing the element of individual diversity.

The formulæ for determining the rate of crossing over p from Q for the several gametic combinations that occurred in these studies are given in Table 2. The calculations were greatly facilitated by a series of curves plotted from the equations.

VARIABILITY OF CROSSOVER RATE

VARIABILITY NOT UNIQUE IN C–Wx LINKAGE NOR IN CHINESE-ALGERIA MAIZE HYBRIDS

That the variability found in the rate of crossing over between *C* and *Wx* is not unique for this pair of linked genes is shown by the results obtained by Emerson and Hutchison (*6*) with the *B–Lg*[6] factor pair, where standard deviations of 4.48 ± 0.49 and 4.49 ± 0.49 were found in the male and female gametes respectively. These are standard deviations comparable with those for the *C–Wx* factors shown in Table 3.

These authors also report on a series of plant reciprocals involving the *C–Sh* genes, where standard deviations of 1.98 ± 0.21 and 2.45 ± 0.26 were found in the male and female gametes. Although both of these standard deviations are lower than most of those obtained with the *C–Wx* genes shown in Table 5, there are several progenies in this table with comparable standard deviations.

[6] *B* is a factor for plant color, and *Lg* is a factor for liguleless leaves.

TABLE 3.—*Summary of the published data on linked seed characters in maize showing variability in crossover rate*

Authority cited	Sex of gametes measured	Number of ears	Number of seeds	Mean percentage of crossover	Observed σ	Coefficient of variation	σ_{so}	σ_{so} corrected for size of population
Kempton (*11*), *C–Wx*	Female and male.	19	9,065	26.60±0.68	4.29±0.47	16.20±1.77	4.85±0.53	5.06±0.55
Bregger (*2*), *C–Wx*	Female	9	3,105	26.70±.76	3.09±.49	11.40±1.80	3.49±.56	3.82±.61
Hutchison (*9*), *C–Wx*	do	12	6,704	21.71±.55	2.62±.36	12.05±1.65	3.18±.44	3.40±.47
Emerson and Hutchison (*6*), *B–Lg.*	Male	19	3,865	38.01±.67	4.18±.46	11.00±1.20	4.30±.47	4.48±.49
	Female	19	4,257	36.58±.67	4.15±.45	11.35±1.24	4.31±.47	4.49±.49
Emerson and Hutchison (*6*), *C–Sh.*	Male	20	5,640	1.86±.08	.54±.06	28.80±3.07	1.98±.21	2.06±.22
	Female	20	10,548	2.98±.13	.83±.09	27.80±2.96	2.45±.26	2.55±.27

Similarly Gowen (*7*) has shown that in Drosophila, with environmental factors relatively constant and heritable differences reduced to a minimum, the percentage of crossing over is highly variable. Using the coefficient of variability Gowen concludes that double crossing over is more variable than single crossing over, but the propriety of using this measure of variability has been questioned (p. 6). If the observed standard deviation (σ) of crossing over is compared with the expected, $\sqrt{pq/H}$, it is clear that double crossing over is less variable than single crossing over. Thus the σ of single crossing over exceeds the expected by 1.61 ± 0.277, whereas the σ of double crossing over is but 0.005 ± 0.048 in excess of that expected. It is evident, however, that single crossing over is highly variable and in excess of that expected, on the assumption that the populations measured were random samples from a single population. Gowen's data are presented in Table 4.

TABLE 4.—*Standard deviations (σ) of percentage of crossing over in the several regions of the third chromosome of Drosophila melanogaster compared with the expected*

[Observed σ from Gowen (*7*)]

Region	σ	$\sqrt{pq/H}$	$\sigma-\sqrt{pq/H}$	D/E
Single crossing over:				
$S_e D'$	3.81±0.12	3.03	0.78±0.12	6.5
$S_e S_s$	6.33±.20	3.90	2.43±.20	12.2
$S_e e^s$	8.28±.26	4.46	3.82±.26	14.7
$S_e r_o$	9.65±.31	4.83	4.82±.31	15.6
$D' C_u$	2.68±.21	1.61	1.07±.21	5.1
$D' S_s$	3.91±.12	2.85	1.06±.12	8.8
$D' e^s$	5.92±.19	3.83	2.09±.19	11.0
$D' r_o$	7.57±.24	4.74	2.83±.24	11.8
$C_u S_s$	1.68±.13	2.21	−.53±.13	4.2
$S_s H'$	2.26±.18	2.88	−.62±.18	3.4
$S_s e^s$	3.79±.12	3.01	.78±.12	6.5
$S_s r_o$	6.10±.19	4.46	1.64±.19	8.6
$H' e^s$	2.32±.18	1.04	1.28±.18	7.1
$e^s r_o$	4.96±.15	3.90	1.06±.15	7.1
Mean			1.608±.277	5.8
Double crossing over:				
$S_s D'$ and $D' SS$	1.03±.03	.99	.04±.03	1.3
$S_s D'$ and $S_s e^s$	.95±.03	1.08	−.13±.03	4.3
$S_s D'$ and $e^s r_o$	1.46±.05	1.16	.30±.05	6.0
$D' S_s$ and $S_s e^s$	.61±.02	.75	−.14±.02	7.0
$D' S_s$ and $e^s r_o$	1.21±.04	1.17	.04±.04	1.0
$S_s e^s$ and $e^s r_o$	.67±.02	.75	−.08±.02	4.0
Mean			.005±.048	.1

The variability of the *C–Wx* linkage relationship seems to be no greater in the hybrids between Chinese maize and the Algeria pop corn used in these studies than in hybrids involving unrelated varieties. Thus the crossing over between *C* and *Wx* as reported by Bregger (*2*) has a standard deviation of 3.82 ± 0.61, and that reported by Hutchison (*9*) has a standard deviation of 3.40 ± 0.47. (Table 3.) There would seem, then, to be no reason to believe that the variability in crossing over between *C* and *Wx* is in any way unique or that it is any greater in the material used by the writers than in that studied by others.

CROSSOVER RATE MORE VARIABLE IN SOME PROGENIES THAN IN OTHERS

A study of a number of progenies discloses the fact that not only do progenies differ in the mean rate of crossing over but also that the stability of the crossover rate varies, some progenies being much more variable in this respect than others. Biometrical constants for several progenies are given in Table 5.

It will be seen that the progenies listed in Table 5, which are limited to those having not fewer than four plants, have standard deviations ranging from 0.78 ± 0.19 to 11.00 ± 1.66; or if the very low one be disregarded because only four plants are involved, the range is from 2.62 ± 0.30 to 11.00 ± 1.66.

A comparison of the expected standard deviation—that is, $\sqrt{pq/H}$, with the σ_{50} corrected for the size of the population—shows that in most cases the variability of the crossover rate is significantly greater than that expected for the individual progenies. A single instance is found where the observed standard deviation (σ_{50p}) is significantly less than the expected, and this is in a group of only four ears. There are several progenies with σ_{50p} but slightly greater than the expected, but of the 48 groups 38 show a variability that exceeds the expected by more than three times the probable error of the difference. The mean of the array of differences is 2.98 ± 0.18, with the observed standard deviations exceeding the expected, and is clearly significant.

There can be no question that in certain progenies the rate of crossing over is remarkably uniform and in others extremely variable, but in general the crossover rate is more variable than would be expected if the variability were due entirely to chance.

The individual diversity among the plants of certain progenies with respect to the rate of crossing over is shown by the series of correlation coefficients in Table 6. The coefficients are all calculated by the formula

$$\frac{\sigma_1^2 + \sigma_2^2 - \sigma_{1-2}^2}{2\sigma_1\sigma_2}$$

where σ_1 and σ_2 are the standard deviations of the two variables weighted by the number of seeds on the ear, and the σ_{1-2} is the standard deviation of the array of differences between the paired observations weighted by $1/E_d^2$. Although based on small numbers, the coefficients give definite evidence that progenies differ in a variety of ways with respect to crossing over.

TABLE 5.—*Percentage of crossing over between C–Wx and standard deviations of crossover percentages for a number of progenies*

Progeny	Heterozygous sex	Number of ears	Number of seeds	Percentage of crossovers	Observed σ	Coefficient of variation	σ_{50}	σ_{50p}	$\sqrt{pq/H}$ [1]	Difference [2] $(\sigma_{50p}-\sqrt{pq/H})$	D/E
Dh 416L3L1C20	Female	14	6,899	32.26±0.81	4.26±0.54	13.22±1.69	4.55±0.58	4.82±0.61	2.44	2.38	3.9
Dh 416L3L1C20	Male	21	11,314	30.18± .65	4.41± .46	14.62±1.52	4.80± .50	4.98± .52	2.22	2.76	5.3
Dh 416L3L1C1L1L22	Female	10	4,659	23.08±1.12	4.82± .72	20.88±3.15	6.00± .90	6.50± .98	2.45	4.05	4.1
Dh 416L3L1C1L1L22	Male	8	2,888	18.91± .11	4.17± .70	22.05±3.71	5.32± .90	5.90± .99	2.67	3.23	3.3
Dh 416L3L1C1L1L1L23	Female	15	5,406	28.43±1.00	5.47± .67	19.30±2.37	6.07± .75	6.40± .79	2.85	3.55	4.5
Dh 416L3L1C1L1L1L23	Male	9	3,103	24.20±1.77	7.20±1.15	29.70±4.72	8.42±1.34	9.22±1.47	3.87	5.35	3.6
Dh 416L3L1C1L1L2L23	Female	9	3,374	31.34±1.98	8.07±1.28	25.80±4.10	8.71±1.39	9.54±1.52	2.79	6.75	4.4
Dh 416L3L1C1L1L2L23	Male	35	10,102	28.22± .87	7.66± .62	27.20±2.19	8.51± .69	8.70± .71	4.62	4.08	5.7
Dh 416L3L1C3L21	Female	6	2,709	27.18±1.67	5.28±1.03	19.43±3.74	5.94±1.16	6.74±1.31	2.44	4.30	3.3
Dh 416L3L1C3L21	Male	8	4,473	24.53±1.47	5.55± .93	22.62±3.82	6.45±1.09	7.14±1.20	2.23	4.91	4.1
Dh 416L3L1C3L1L22	Female	9	4,658	29.49± .94	3.83± .61	12.99±2.07	4.20± .67	4.60± .73	2.26	2.34	3.2
Dh 416L3L1C3L1L22	Male	5	2,266	22.12±1.60	4.46± .95	20.15±4.30	5.38±1.15	6.40±1.37	2.42	3.98	2.9
Dh 416L3L1C1L1L3L23	Female	12	5,509	29.35± .97	4.64± .64	15.80±2.17	5.10± .70	5.45± .75	2.39	3.06	4.1
Dh 416L3L1C1L1L3L23	Male	15	3,256	31.14± .92	4.98± .61	16.00±1.97	5.38± .66	5.67± .70	4.70	.97	1.4
Dh 416L3L1C4L1L23	Female	10	3,650	18.88± .99	4.28± .65	22.70±3.42	5.47± .83	5.92± .89	4.11	1.81	2.0
Dh 416L3L1C4L1L23	Male	4	678	17.26± .20	.47± .12	2.70± .64	.62± .15	.78± .19	5.82	−5.04	26.5
Dh 416L3L1C5L21	Female	5	4,068	32.57±2.65	7.39±1.58	22.75±4.85	7.88±1.68	9.37±2.00	1.86	7.51	3.8
Dh 416L3L1C5L21	Male	5	7,352	29.65±3.22	8.97±1.91	30.25±6.45	9.81±2.10	8.24±1.76	1.32	6.92	3.9
Dh 416L3L1C5L3L22 *R R* [3]	Female	5	2,132	18.49±1.16	3.22± .69	17.42±3.72	4.15± .89	4.94±1.05	3.37	1.57	1.5
Dh 416L3L1C5L3L22 *R R*	Male	4	1,913	24.48±2.12	5.01±1.20	20.50±4.90	5.83±1.39	7.31±1.74	2.33	4.98	2.9
Dh 416L3L1C5L3L22 *R r*	Selfed	8	4,149	17.48± .83	3.13± .53	17.93±3.03	4.13± .70	4.58± .77	2.16	2.42	3.1
Dh 416L3L1C5L3L1R23 *R R*	Female	41	19,759	20.77± .54	5.11± .38	24.62±1.84	6.29± .47	6.41± .48	3.31	3.10	6.5
Dh 416L3L1C5L3L1R23 *R r*	do	26	14,258	20.19± .61	4.63± .48	22.92±2.39	5.76± .54	5.94± .56	2.23	3.71	6.6
Dh 416L3L1C5L3L1R23 *R R*	Male	60	27,725	19.14± .37	4.22± .26	22.05±1.36	5.37± .33	5.44± .33	2.70	2.74	8.3
Dh 416L3L1C5L3L1R23 *R r*	do	56	24,202	16.97± .41	4.50± .29	26.50±1.69	5.99± .38	6.07± .39	2.86	3.21	8.2
Dh 416L3L1C5L3L1R23 *R R*	Selfed	9	4,455	21.48±1.20	4.89± .78	23.78±3.78	5.94± .94	6.50±1.03	2.49	4.01	3.9
Dh 416L3L1C5L3L1R23 *R r*	do	11	3,156	19.12± .88	4.03± .58	21.07±3.05	5.12± .74	5.50± .79	3.22	2.28	2.9
Dh 416L3L1C5L3L2R23 *R R*	Female	9	4,710	24.34±1.34	5.43± .86	22.30±3.54	6.30±1.00	6.90±1.10	3.24	3.66	3.3
Dh 416L3L1C5L3L2R23 *R r*	do	14	6,763	21.20±1.08	5.67± .72	26.75±3.41	6.94± .89	7.34± .94	3.26	4.08	4.3
Dh 416L3L1C5L3L2R23 *R R*	Male	5	2,225	27.18±1.52	4.23± .90	15.57±3.32	4.75±1.01	5.61±1.20	2.44	3.17	2.6
Dh 416L3L1C5L3L2R23 *R r*	do	8	2,588	25.44±1.63	6.17±1.04	24.25±4.09	7.09±1.20	7.85±1.32	4.00	3.85	2.9
Dh 416L3L1C5L3L2R23 *R R*	Selfed	6	2,023	23.77±1.25	3.93± .77	16.54±3.20	4.61± .90	5.31±1.03	3.63	1.68	1.6
Dh 416L3L1C5L3L2R23 *R r*	do	5	1,477	24.80±2.17	6.04±1.29	24.35±5.20	7.00±1.49	8.33±1.78	4.06	4.27	2.4
Dh 416L3L1C5L4L23	Female	17	7,610	38.25± .42	2.43± .27	6.35± .73	2.50± .29	2.62± .30	2.64	−.02	.1
Dh 416L3L1C5L4L23	Male	37	18,421	37.14± .30	2.73± .21	7.36± .59	2.83± .30	2.89± .31	2.42	.47	1.5
Dh 416L3L1C5L4L1L24	Female	52	15,760	36.00± .40	4.23± .28	11.75± .77	4.41± .29	4.47± .29	3.40	1.07	3.7
Dh 416L3L1C5L4L1L24	Male	30	10,716	37.30± .38	3.05± .27	8.19± .71	3.15± .27	3.23± .28	4.17	−.94	3.4
Dh 417L1L2L1L21	Female	14	5,532	19.97± .95	4.96± .63	24.83±2.14	6.21± .79	6.58± .84	2.62	3.96	4.7
Dh 417L1L2L1L21	Male	12	4,640	16.86± .54	2.62± .36	15.55±2.14	3.50± .48	3.74± .52	2.67	1.07	2.0
Dh 417L1L2L1L21	Selfed	10	3,514	20.05±1.29	5.56± .84	27.73±4.18	6.96±1.05	7.54±1.14	3.09	4.45	3.9

[1] $p=q=0.5$.

[2] $\sigma_{50p}=\sigma_{50}$ corrected for size of population.

[3] *R* is a factor for aleurone color.

TABLE 5.—*Percentage of crossing over between C–Wx and standard deviations of crossover percentages for a number of progenies*—Continued

Progeny	Heterozygous sex	Number of ears	Number of seeds	Percentage of crossovers	Observed σ	Coefficient of variation	σ_{50}	σ_{50p}	$\sqrt{pq/H}$	Difference $(\sigma_{50p}-\sqrt{pq/H})$	D/E
Dh 417L1L2L1L2L23	Female	22	6,628	25.60±0.92	6.25±0.64	24.40±2.48	7.16±0.73	7.44±0.76	3.16	4.28	5.6
Dh 417L1L2L1L2L23	Male	19	5,668	28.00± .97	6.03± .66	21.50±2.35	6.72± .74	7.00± .77	3.47	3.53	4.6
Dh 417L1L2L1L2L23	Selfed	10	3,611	20.80±1.92	8.26±1.24	39.71±4.35	10.16±1.53	11.00±1.66	4.11	6.89	4.1
Ph 230L1 and L2R24 *R R*	Female	20	10,374	21.59± .69	4.57± .49	21.20±2.26	5.55± .59	5.77± .61	2.67	3.10	5.1
Ph 230L1 and L2R24 *R r*	do	29	9,933	17.70± .70	5.59± .49	31.60±2.80	7.33± .65	7.53± .67	3.04	4.49	6.7
Ph 230L1 and L2R24 *R r*[1]	do	4	1,285	15.46±2.56	6.07±1.45	39.25±9.35	8.38±2.00	10.51±2.51	3.26	7.25	2.9
Ph 230L1 and L2R24 *R R*	Male	21	5,883	26.19±1.10	7.66± .80	29.25±3.04	8.72± .91	9.05± .94	3.68	5.37	5.7
Ph 230L1 and L2R24 *R r*	do	15	5,654	26.73± .89	4.84± .60	18.12±2.23	6.28± .77	9.19±1.13	3.03	6.16	5.4
Mean										3.01±0.18	16.7

[1] 75 per cent white.

The data from a single progeny at Lanham, Md., in 1924, shows a sensible correlation between the percentage of crossing over in two samples of the same heterozygous pollen as well as a correlation between the rate in upper and lower ears when the male parent is heterozygous. (Table 6.)

These correlations can be interpreted only as resulting from factors operating upon the male gametes, since in the same material no correlation was found between the percentage of crossing over in the male and female gametes. The absence of a positive correlation in this latter instance shows that there are no genetic factors affecting both sexes in so far as this one progeny is concerned, and it also shows that environmental factors did not differentiate the individuals before the separation of the sexes. This conclusion derives further support from the lack of correlation between the percentage of crossing over on upper and lower ears where the female parent was heterozygous, thus indicating an absence of heterozygous genetic factors affecting the crossing over in one sex.

An entirely different situation prevailed at Arlington, Va., in 1923, with two progenies closely related to that grown at Lanham, Md., in 1924. Here high correlations were found between the percentage of crossing over on butts and tips where the female parent was heterozygous or homozygous, as well as between the percentage of crossing over in upper and lower ears when the male was heterozygous and also between male and female gametes. From these correlations it is not possible to determine whether genetic or general environmental factors are the causal agents, but it is evident that one or the other or both are differentiating the individuals with respect to the rate of crossing over.

A similar condition is indicated for the crossing over between *B* and *Lg* and *C* and *Sh* reported by Emerson and Hutchinson (*6*). In the case of each of these linked pairs, sensible correlations are found between the percentage of crossing over in the male and female gametes.

TABLE 6.—*Correlations between percentages of crossing over in two samples of gametes*

Correlation of percentage of crossing over between—	Number of plants	Product moment coefficient of correlation (r)
C and *Wx* in two samples of same pollen, Lanham, 1924	13	0.500±0.145
C and *Wx* in male and female gametes, Lanham, 1924	17	−.333± .147
C and *Wx* in upper and lower ears, female heterozygous, Lanham, 1924	17	−.328± .146
C and *Wx* in upper and lower ears, male heterozygous, Lanham, 1924	10	.780± .083
C and *Wx* in butts and tips, female heterozygous, Arlington, 1923, progeny 1	43	.662± .058
C and *Wx* in butts and tips, female heterozygous, Arlington, 1923, progeny 2	26	.541± .093
C and *Wx* in butts and tips, male heterozygous, Arlington, 1923, progeny 2	10	.962± .016
C and *Wx* in upper and lower ears, male heterozygous, Arlington, 1923, progeny 1	8	.817± .079
C and *Wx* in male and female gametes, Arlington, 1923, progeny 1	34	.678± .062
B and *Lg* in male gametes with that of female, Emerson and Hutchinson (*6*)	19	.380± .117
C and *Sh* in male gametes with that of female, Emerson and Hutchinson (*6*)	20	.597± .091
C and *Wx* in upper and lower ears, male heterozygous, Ph 230L1 and L2R24	10	.249± .200
C and *Wx* in upper and lower ears, female heterozygous, Ph 230L1 and L2R24	32	.483± .091

VARIABILITY OF CROSSING OVER NO GREATER IN MALE THAN IN FEMALE GAMETES

As a means of determining whether the male gametes are more subject to environmental influences than the female gametes, the

standard deviations of the percentage of crossing over in the two sexes may be examined. These have been assembled in Table 7 for 13 progenies where reciprocal crosses between identical plants were available. Since the rate of crossing over is not alike for the two sexes, and to avoid a spurious difference due to the error inherent in the calculation of standard deviations of percentages centered at other than 50 per cent, the observed standard deviations have been corrected to a basis of 50 per cent.

Table 7 shows that there is on the average a slightly greater variability in the female than in the male gametes, but the difference is not statistically significant. None of the individual progenies showed a significant difference, and it seems safe to conclude that the variability of crossing over is no greater in one sex than in the other.

TABLE 7.—*Standard deviations of the percentage of crossing over in male and female gametes*

[Comparison restricted to reciprocal crosses]

Progeny	Female gametes					Male gametes				Difference ($\sigma_{50♀} - \sigma_{50♂}$)
	Number of ears	Number of seeds	Percentage of crossovers	σ	σ_{50}	Number of seeds	Percentage of crossovers	σ	σ_{50}	
Dh 416L3L1C1L1L22	4	1,919	24.75	2.96±0.71	3.43±0.82	1,885	20.53	2.04±0.49	2.53±0.60	0.90±0.99
Dh 416L3L1C1L1L1L23	7	3,400	25.80	4.65± .84	5.31± .96	2,104	24.50	6.51±1.17	7.57±1.36	−2.26±1.67
Dh 416L3L1C1L1L2L23	8	3,064	31.41	6.78±1.14	7.32±1.23	2,722	32.36	6.10±1.03	6.52±1.03	.80±1.61
Dh 416L3L1C1L1L3L23	7	2,933	31.00	4.50± .81	4.86± .88	1,387	30.50	5.87±1.06	6.37±1.15	−1.51±1.45
Dh 416L3L1C3L21	5	2,331	27.16	5.70±1.21	6.41±1.37	4,100	23.20	4.33± .92	5.13±1.09	1.28±1.75
Dh 416L3L1C3L1L22	5	3,296	28.25	3.87± .83	4.30± .92	2,266	22.11	4.46± .95	5.38±1.14	−1.08±1.47
Dh 416L3L1C5L21	5	4,068	32.57	7.39±1.58	7.88±1.68	7,352	29.65	8.97±1.91	9.81±2.10	−1.93±2.62
Dh 416L3L1C5L4L23	7	3,523	39.40	3.21± .58	3.29± .59	3,661	35.80	2.22±1.07	2.32± .42	.97± .72
Dh 416L3L1C5L4L1L24	17	7,336	35.50	2.91± .34	3.04± .35	6,300	37.60	2.93± .34	3.02± .35	.02± .49
Dh 416L3L1C5L3L1R23	49	24,627	20.47	5.24± .36	6.49± .44	27,517	18.07	4.02± .28	5.22± .36	1.27± .57
Dh 416L3L1C5L3L2R23	11	5,284	22.16	5.68± .82	6.82± .98	3,683	27.42	3.98± .57	4.46± .64	2.36±1.17
Dh 417L1L2L1L21	13	4,995	20.62	4.83± .64	5.95± .79	4,693	16.71	2.71± .36	3.63± .48	2.32± .92
Dh 417L1L2L1L2L23	13	4,122	25.10	4.18± .55	4.81± .64	3,757	29.30	4.64± .61	5.10± .95	− .29±1.15
Mean										.628±.212

In 4 of the 13 progenies the rate of crossing over is higher in the male than in the female gametes. If the difference between the crossover rates is assumed to be due to a differential viability of the gametes, the variability of crossing over would be expected

to be greater in the male gametes when the crossing over was low in the males. Conversely, the variability should be greater in the female gametes when crossing over is low in the female. The data have been analyzed from this standpoint. The seven progenies having less crossing over in the male than in the female gametes have a mean difference in $\sigma_{50}(\sigma_{50}\,♀ - \sigma_{50}\,♂)$, with the female gametes more variable, of 0.839 ± 0.286; and the four progenies in which the crossing over in the female gametes was less than that of the male have a mean difference in σ_{50}, also with the female gametes more variable, of 0.312 ± 0.334. The difference of 0.525 ± 0.439 between the two groups is not significant. Contrary to the hypothesis, the crossover rate in the female gametes is more variable when the percentage of crossing over is higher in the female than in the male gametes, but the difference between the mean of this group of 7 progenies and that of the whole population of 13 is but 0.211 ± 0.356. There would thus seem to be no support for the idea that high variability is associated with a low rate of crossing over.

VARIABILITY OF CROSSING OVER NO GREATER IN UPPER THAN IN LOWER EARS

Although differences in the rate of crossing over between upper and lower ears are found in certain progenies, there are no consistent differences in the variability of the crossover rate in upper and lower ears. The standard deviation of the crossover ratio in upper and lower ears is practically the same, and this holds whether the heterozygous sex is male or female. The data for upper and lower ear groupings for three progenies are shown in Table 8.

As in the comparison of variability in the two sexes, the absence of any correlation between the degree of variability and the apparent rate of crossing over indicates that a differential death rate of gametes or zygotes is not an important factor.

TABLE 8.—*Comparison of variability* (σ_{50}) *in percentage of crossing over in upper and lower ears*

Progeny	Upper ears			Lower ears			Difference (σ_{50} upper − σ_{50} lower)
	Percentage of crossovers	σ	σ_{50}	Percentage of crossovers	σ	σ_{50}	
Male gametes:							
Dh 416L3L1C5L3L1R23	18.3	3.92	5.07±0.85	20.2	2.83	3.52±0.59	1.55±1.04
Ph 230L1 and L2R24	24.8	4.68	5.41± .82	28.1	5.89	6.55± .99	−1.41±1.28
Dh 416L3L1C5L4L1L24	37.4	2.73	2.82± .43	37.5	2.13	2.20± .33	.62± .54
Female gametes:							
Ph 230L1 and L2R24	18.8	5.38	6.88± .58	19.7	5.77	7.26± .49	− .38± .76
Dh 416L3L1C5L4L1L24	36.0	2.64	2.75± .32	34.8	3.19	3.34± .39	− .59± .50

VARIABILITY OF CROSSING OVER NO GREATER IN THE BASE THAN IN THE TIP OF THE EAR

In two progenies the lower and upper halves of the ear were classified separately. In one progeny this procedure was followed for both male heterozygous and female heterozygous plants, but in the other only the female heterozygous plants were so treated.

The classification obtained from these divisions furnishes data from which the relative variability in percentage of crossing over of the two halves of the ear can be measured.

In all three cases (male and female gametes from one progeny and female gametes from the other) crossing over proved to be more variable in the tip than in the base of the ear, but in none of the cases was the difference significant. The mean difference $(\sqrt{\Sigma\sigma^2 N/\Sigma N})$ is 1.22 ± 0.56.

It would seem, therefore, from the present data that one part of the ear is as variable as the other with respect to the rate of crossing over. The data are presented in Table 9.

TABLE 9.—*Comparison of variability* (σ_{50}) *of percentage of crossing over in the tip and the base of the ear*

Progeny	Number of ears	Tip			Base			Difference (σ_{50} tip—σ_{50} base)
		Percentage of crossovers	σ	σ_{50}	Percentage of crossovers	σ	σ_{50}	
Female gametes:								
Dh 416L3L1C5L3L1R23----	43	22.10	6.19	7.46±0.54	20.68	5.27	6.51±0.47	0.95±0.70
Dh 416L3L1C5L3L2R23----	26	24.02	7.62	8.82± .83	21.49	5.53	6.72± .63	2.10±1.04
Male gametes:								
Dh 416L3L1C5L3L2R23----	10	27.28	7.05	7.90±1.19	28.19	7.10	7.88±1.19	.02±1.68

CROSSING OVER GENERALLY LESS VARIABLE IN SEVERAL SAMPLES OF THE SAME INDIVIDUAL THAN IN SINGLE SAMPLES FROM SEVERAL INDIVIDUALS

In narrowing the field of factors that might bear a causal relationship to the variation in crossover percentages, it became of interest to compare the variability as measured in a progeny of plants with that of several measures of individual plants from the same progeny.

It seldom happens that a single plant serves as a parent for more than two ears, but the records afford two cases where plants served as male parents in four and five pollinations.

Many progenies are available where single plants have functioned twice as male parents, and two progenies furnish material where single plants have functioned twice as female parents.

These paired samples can be used to calculate the relative variability of samples from single plants as compared with that of several plants. If two samples of gametes from an individual are as unlike, on the average, as the means of the individuals, then the standard deviation (σ) of the differences between pairs should equal the standard deviation of the sum.

These comparisons have been made for a number of progenies and various sorts of paired samples in Table 10.

For some of these progenies the same relationship is indicated by the correlation between samples as shown in Table 6 (p. 13).

The first five entries in Table 10 are drawn from upper and lower ear groupings and are limited to pollinations made on the same day. Those where the male parent is heterozygous are further limited to the same double recessive parent, thus obviating any

effect that the homozygous recessive parent might have on the gametic proportions. In entries 6 to 9 of the table the data are assembled without respect to whether the two pollen samples were applied on the same day or to the same double recessive parent.

TABLE 10.—*Comparison of the variability of crossing over in a population with that of samples from single individuals*

[Comparison is made between the standard deviation (σ) of the differences between paired samples and that of the sums of the samples and also between the upper and the lower halves of the ears]

Progeny	Sex of gametes	Number of ears	Number of pairs	σ difference	σ sum	Difference (σ sum$-\sigma$ difference)	D/E
Paired samples:							
(1) Dh 416L3L1C5L3L1R23	Male		8	2.30±0.39	7.14±1.20	4.84±1.26	3.8
(2) Ph 230L1 and L2R24	do		10	5.47± .83	8.38±1.26	2.91±1.51	1.9
(3) Dh 416L3L1C5L4L1L24	do		10	1.72± .26	4.46± .68	2.74± .73	3.8
(4) Ph 230L1 and L2R24	Female		32	5.59± .47	9.52± .80	3.93± .93	4.2
(5) Dh 416L3L1C5L4L1L24	do		17	4.77± .55	3.40± .40	−1.37± .68	2.0
(6) Dh 416L3L1C5L4L1L24	Male		13	3.53± .47	5.92± .78	2.39± .90	2.7
(7) Dh 416L3L1C5L3L1R23	do		16	2.58± .31	9.72±1.16	7.14±1.20	6.0
(8) Dh 416L3L1C1L1L2L23	do		8	3.61± .61	11.00±1.86	7.39±1.96	3.8
(9) Dh 416L3L1C5L4L23	do		8	3.65± .62	4.46± .76	.81± .98	0.8
Ear base and tip samples:							
(10) Dh 416L3L1C5L3L1R23	Female	43		4.75± .35	10.84± .78	6.09± .85	7.2
(11) Dh 416L3L1C5L3L2R23	do	26		6.56± .61	11.58±1.08	5.02±1.24	4.1
(12) Dh 416L3L1C5L3L2R23	Male	10		1.90± .29	14.10±2.12	12.20±2.14	5.7

Table 10 shows that in general the samples of gametes from the same individual are less variable than the population as a whole. It is equally obvious, however, that in some progenies the samples are not less variable. In these cases it will be noted that the standard deviations are relatively low, and as a matter of fact in these progenies no correlation in the rate of crossing over is found between the paired samples, indicating that the progenies have reached genetic uniformity with respect to crossing over.

As a further check on the relative variability of the percentage of crossing over in several samples of a single individual compared with that of single samples of several individuals, two plants are available in a single progeny from one of which five samples of pollen were taken and from the other four samples were taken. These samples are all of the male gametes, and the standard deviations may be compared with that of the population of male gametes as a whole for this progeny. The plant from which five samples of pollen were taken had a standard deviation (σ_{50}) of 2.78 ±0.59 and that furnishing four samples had a standard deviation of 4.50 ±1.07 (corrected for size of population). These standard deviations (Table 11) are to be compared with that of 2.82 ±0.22 for the population as a whole. In this progeny, therefore, it would seem that the individual plants did not vary among themselves in the rate of crossing over to an extent greater than did the several samples of single individuals. This conclusion is further supported by the results cited in entry 9 in Table 10 where two samples of pollen were used from each of eight plants in this same progeny.

Additional comparisons between the variability of individuals and that of the samples from a single individual are afforded by three lots of ears in which the upper and lower halves were classified

separately. In all three lots the variability between the base and tip samples was less than that of the individual plants. The data are included in Table 10 (entries 10–12).

TABLE 11.—*Comparison of variability of crossing over in a population with that of samples from single individuals in the same population*

Progeny	Standard deviations corrected for size of population		
	5 samples from 1 plant	4 samples from 1 plant	Entire population, 37 plants
Dh 416L3L1C5L4-1-L23	2.78±0.59	4.50±1.07	2.82±0.22

In most progenies, therefore, there seems to be no question that the variability in crossover rate for the population as a whole is greater than that found in samples of gametes from individual plants. Exceptions have been noted, but in these cases the variability of the crossover ratio was relatively low.

CROSSING OVER LESS VARIABLE IN SAMPLES FROM DIFFERENT PARTS OF THE SAME MALE INFLORESCENCE THAN IN SAMPLES FROM SEVERAL INFLORESCENCES

Samples of pollen were collected separately from several parts of a maize tassel and applied to the silks of double-recessive plants. The data are given in Table 12. Unfortunately, several of the pollinations resulted in very few seeds, thus precluding any very exact determinations of differences in rate of crossing over between the sections of the inflorescence, though the greatest difference is 10.4 per cent. The material can be utilized to compare the variability of the crossover rate with that expected if the several pollinations were samples of the same population and also with that obtained in the progeny of which this plant was a single representative. The standard deviation corrected for size of population (σ_{50}) is 4.73±0.92 and the $\sqrt{pq/H}$ is 6.52, the crossover ratio being no more variable than is to be expected in samples of this size. The σ_{50} for the male gametes of the progeny is 8.70±0.71, from which the σ_{50} of this plant departs by 3.97±1.16. Clearly, in this progeny the variability of crossing over, as measured in several parts of a single inflorescence, is less than that obtained with single measures of several plants.

TABLE 12.—*Crossing over in different parts of the tassel of a single maize plant*

Parts of tassel	Number of seeds	Percentage of crossovers
Central spike	395	27.1±1.50
Uppermost tassel branch	305	22.6±1.61
Branch 2	257	29.6±1.92
Branch 4	64	26.6±3.72
Branch 6	176	31.8±2.36
Branch 10	14	21.4±7.40
Mean		27.09±1.16
σ_{50}		4.73± .92
$\sqrt{pq/H}$		6.52
σ_{50} for progeny of which this is one plant		8.70± .71

Altenburg (*1*), working with *Primula sinensis*, measured the gametic proportions separately for individual anthers of a single plant. The number of offspring resulting from pollinations with single anthers was small, and in consequence only very large differences in crossover rate could have been detected. Using his data for the crossing over between *L* and *S*[7] for the plant 4.2a, percentages ranging from 39.9±3.67 to 54.2±2.92 are disclosed. This range is found between two anthers from the same flower and is of magnitude comparable with the large differences found between plants of maize. It can not be considered significant, however, in view of the errors and the fact that it is the largest difference of a possible 21. The data are shown in Table 13.

The variability of crossing over in the six anther samples is as great as that found between individual plants in many maize progenies but the excess beyond the expected standard deviation (σ) is not significant.

TABLE 13.—*Gametic proportions in individual anthers of a single plant of Primula sinensis*

[From Altenburg (*1*) Table 2; 4.2a is plant number; 1 and 2 represent flower numbers; 2–1 to 5 represent anther numbers; samples in entries 2–6 are of anthers from a single flower]

Entry No. and anther	Gametic proportions					Percentage of—		
	L S	*L s*	*l S*	*l s*	Total	*l*	*s*	Crossovers
(1) 4. 2a 1–2	43	23	37	36	139	35. 2	52. 5	42. 6±2. 83
(2) 4. 2a 2–1	34	44	28	26	132	40. 9	53. 1	54. 2±2. 92
(3) 4. 2a 2–2	49	52	37	52	190	46. 9	54. 7	46. 5±2. 44
(4) 4. 2a 2–3	21	22	12	23	78	44. 9	57. 7	42. 5±3. 78
(5) 4. 2a 2–4	26	21	12	22	81	42. 0	53. 1	39. 9±3. 67
(6) 4. 2a 2–5	18	16	14	17	65	47. 7	50. 8	46. 1±4. 17
Mean								45. 92±1. 45
σ_{s0}								5. 35±1. 04
$\sqrt{pq/H}$								5. 02

VARIABILITY OF CROSSING OVER NO GREATER IN OLD THAN IN FRESH POLLEN

Age-of-pollen experiments, in which samples of pollen were collected early in the morning and each sample divided into two equal lots, one lot being used immediately and the other being held for about seven hours, furnish data suitable for determining the relative variability of the crossover ratio in fresh and old pollen.

Successful paired pollinations were obtained from 13 plants. From these plants the fresh pollen had a σ_{50} of 3.39±0.45 and the old pollen a σ_{50} of 3.72±0.50. The difference, 0.33±0.67, though in the direction of the crossover ratio, being more variable in old pollen, is not statistically significant.

CROSSING OVER NO MORE VARIABLE IN FIRST THAN IN LAST GAMETES FORMED

From the available evidence on the relative variability of the crossover ratio in young and old plants, it is not possible to detect small differences in variability, since only seven plants functioned as early and late parents. The difference observed is in the direc-

[7] *L* is a factor for style length and *S* is a factor for stigma color.

tion of the crossover rate being more variable in the early than in the late gametes. The difference is 2.37±1.99, which, of course, is not statistically significant.

CROSSOVER RATIO MORE VARIABLE THAN MENDELIAN RATIOS

It has been shown that crossing over, as measured by the percentage of individuals in the crossover classes, has a variability not to be ascribed to errors of random sampling.

If this variability results from irregularities in the mechanism of crossing over or from a differential death rate of crossover gametes or zygotes, the percentage of crossing over should be more variable than the Mendelian ratios expressed as percentages.

TABLE 14.—*Comparison of the variability of the crossover rate with that of the percentage of the Mendelian character waxy endosperm in female and male gametes*

Progeny	Number of ears	Number of seeds	Crossover		Waxy		Difference $\sigma_{50CO}-\sigma_{WX}$
			Per cent	σ_{50}	Per cent	σ	
Female gametes:							
Dh 416L3L1C1L1L22	4	1,919	24.75	3.43±0.82	49.4	2.87±0.68	0.56±1.07
Dh 416L3L1C1L1L1L23	7	3,400	25.80	5.31± .96	49.6	1.44± .26	3.87± .99
Dh 416L3L1C1L1L2L23	8	3,064	31.41	7.32±1.23	51.2	2.59± .44	4.73±1.31
Dh 416L3L1C1L1L3L23	7	2,933	31.00	4.86± .88	48.5	1.66± .30	3.20± .93
Dh 416L3L1C3L21	5	2,331	27.16	6.41±1.37	50.1	1.29± .28	5.12±1.40
Dh 416L3L1C3L1L22	5	3,296	28.25	4.30± .92	50.0	.97± .21	3.33± .94
Dh 416L3L1C5L21	5	4,068	32.57	7.88±1.68	48.7	1.88± .40	6.00±1.73
Dh 416L3L1C5L4L23	7	3,523	39.40	3.29± .59	49.8	4.52± .82	−1.23±1.01
Dh 416L3L1C5L4L1L24	17	7,336	35.50	3.04± .35	49.2	2.11± .24	.93± .43
Dh 416L3L1C5L3L1R23	49	24,627	20.47	6.49± .44	50.3	2.34± .16	4.15± .47
Dh 416L3L1C5L3L2R23	11	5,284	22.16	6.82± .98	49.4	1.66± .24	5.16±1.01
Dh 417L1L2L1L21	13	4,995	20.62	5.95± .79	49.9	2.80± .37	3.15± .87
Dh 417L1L2L1L2L23	13	4,122	25.10	4.81± .64	51.3	3.51± .46	1.30± .79
Mean							2.60± .34
Male gametes:							
Dh 416L3L1C1L1L22	4	1,885	20.53	2.53±0.60	51.1	2.35±0.56	0.18±0.82
Dh 416L3L1C1L1L1L23	7	2,104	24.50	7.57±1.36	49.8	1.70± .31	5.87±1.39
Dh 416L3L1C1L1L2L23	8	2,722	32.36	6.52±1.03	49.6	2.93± .49	3.59±1.14
Dh 416L3L1C1L1L3L23	7	1,387	30.50	6.37±1.15	49.0	2.50± .45	3.87±1.23
Dh 416L3L1C3L21	5	4,100	23.20	5.13±1.09	56.0	4.33± .92	.80±1.43
Dh 416L3L1C3L1L22	5	2,266	22.11	5.38±1.14	54.1	1.75± .37	3.63±1.20
Dh 416L3L1C5L21	5	7,352	29.65	9.81±2.10	48.5	1.49± .32	8.32±2.12
Dh 416L3L1C5L4L23	7	3,661	35.80	2.32± .42	47.7	2.70± .49	−.38± .64
Dh 416L3L1C5L4L1L24	17	6,300	37.60	3.02± .35	46.7	3.44± .40	−.42± .53
Dh 416L3L1C5L3L1R23	49	27,517	18.07	5.22± .36	48.1	3.17± .22	2.05± .42
Dh 416L3L1C5L3L2R23	11	3,683	27.42	4.46± .64	46.3	3.62± .52	.84± .82
Dh 417L1L2L1L21	13	4,693	16.71	3.63± .48	50.2	2.88± .38	.75± .61
Dh 417L1L2L1L2L23	13	3,757	29.30	5.10± .95	49.3	3.07± .41	2.03±1.03
Mean							1.28± .31
Combined sexes							1.93± .24

There may be some question as to the propriety of comparing the standard deviations of crossover percentages with those of the percentages of the Mendelian characters, since the deviations of the latter are strictly limited. Thus, if the percentages of the Mendelian characters depart widely from the expected, a gametic composition that will explain the observed ratios is hypothecated. This is especially true in dealing with aleurone color where six factors are recognized. No such procedure is possible in the present stage of our knowledge of linkage relations, and if the crossover percentages

are more variable than the percentages of the Mendelian characters it may mean that crossing over is more sensitive to environmental conditions than simple segregation, or that unrecognized genetic factors affecting the crossover rate are present.

At the present time no genetic factors modifying the waxy-nonwaxy ratio have been identified, and in this respect the waxy character is comparable to the crossover rate between *C* and *Wx*.[8] By limiting the comparison of variability to the waxy character, the objection based on the reduction in variability due to assumed gametic compositions for widely aberrant ratios is partially overcome. Comparisons of this nature are shown in Table 14 where the σ_{50} of the percentage of crossovers is compared with the standard deviation of the percentage of waxy for male and female gametes separately. All comparisons are limited to reciprocal back-crossed ears where the expected percentage of waxy is 50. Although many of the differences shown in this table are not significant, and three instances occur where the standard deviation of the waxy percentages is greater than the corresponding σ_{50} of the percentage of crossing over, taken as a whole there is in each sex a significantly greater variability in the crossover percentage than in the percentage of waxy seeds. Combining the two sexes, the mean difference becomes 1.93 ± 0.24, clearly a significant difference.

In general, then, it may be stated that the crossing over of the factors *C* and *Wx* is more variable than the simple segregation of these characters, but whether this greater variability is due to genetic or environmental factors or both can not be determined from the data thus far submitted.

VARIABILITY IN THE CROSSOVER CLASS NOT THE RESULT OF DIFFERENTIAL DEATH RATE OF ZYGOTES

In hybrids involving two linked characters it is possible to produce F_2 progenies with all four classes in equal numbers. This condition results when one parent is homozygous recessive for one of the characters and heterozygous for the other while the second parent has the reciprocal of this factorial composition. When one of the characters is a dihybrid, hybrids heterozygous for the nonlinked gene of the dihybrid character and homozygous for the linked gene also will produce the four classes with no opportunity for linkage to be expressed. If the increased variability in the apparent rate of crossing over is due to a differential death rate of zygotic classes, we should find in progenies combined in either of the above ways a variability in the percentage of crossover classes comparable with that of progenies showing linkage.

In Table 15 there has been brought together from published data a summary of progenies segregating into all four classes with no opportunity for linkage and progenies of similar parentage combined in a way to exhibit linkage. To these have been added four groups of ears descended from a self-pollinated plant that was heterozygous for both *C* and *Wx*. Two of the groups are reciprocals measuring

[8] Brink (4) has presented evidence to show that the ratio of waxy to nonwaxy is modified when the *Su* factor for sweet endosperm is homozygous recessive and states also that the I aleurone factor influences this ratio. Neither of these factors was involved in the present study, and though other factors present in our experiments may be found to affect the proportion of the waxy seeds, they are still unrecognized and their action appears to be uniform.

linkage in the two sexes. The other two represent the reciprocal combinations that produce all four combinations without linkage.

TABLE 15.—*Comparison of the variability of the percentage of crossing over with that of the Mendelian characters*

Entry number and progeny	Page citation, Kempton (*11*)	Number of ears	Number of seeds	White		Waxy		Crossovers	
				Per cent	Standard deviations (σ)	Per cent	Standard deviations (σ)	Per cent	Standard deviations (σ)
Back-crossed ears:									
(1) *C c wx wx* on *c c Wx wx*	85, 87	21	9, 961	50. 3±0. 37	2. 51±0. 26	49. 4±0. 36	2. 45±0. 26	50. 5±0. 27	1. 81±0. 19
(2) *C c Wx wx* on *c c wx wx*	85, 87	19	9, 065	50. 3± . 39	2. 40± . 26	49. 7± . 44	2. 70± . 30	26. 6± . 78	[1] 4. 85± . 53
(3) Homozygous for *C*, heterozygous for *R*	76	26	10, 011	48. 7± . 51	3. 84± . 40	50. 2± . 47	3. 56± . 37	51. 5± . 47	3. 58± . 37
Selfed ears:									
(4)	70	37	20, 483	26. 3± . 20	[1] 1. 84± . 14	24. 2± . 25	[1] 2. 30± . 18	50. 1± . 62	3. 81± . 30
Back-crossed ears, Lanham, 1924 (Dh 416L3L1-C5L4L1L24):									
(5) Colored horny ♀× white waxy ♂	-------	52	15, 760	48. 6± . 28	3. 03± . 22	49. 9± . 33	3. 53± . 23	36. 0± . 40	[1] 4. 40± . 29
(6) White waxy ♀× colored horny ♂	-------	30	10, 716	48. 3± . 33	2. 68± . 23	46. 3± . 38	3. 08± . 27	37. 3± . 38	[1] 3. 15± . 27
(7) White horny ♀× colored waxy ♂	-------	[2] 19	6, 657	48. 2± . 40	2. 46± . 27	50. 0± . 39	2. 41± . 26	50. 7±1. 10	3. 14± . 34
(8) Colored waxy ♀× white horny ♀	-------	[3] 23	8, 124	49. 5± . 46	3. 25± . 32	45. 3± . 30	2. 14± . 21	49. 4± . 36	2. 58± . 26

[1] Standard deviations (σ) corrected to 50 per cent.
[2] ♀ *c c Wx wx*, ♂ *C c wx wx*.
[3] ♀ *C c wx wx*, ♂ *c c Wx wx*.

There are two instances in Table 15 where the relation of linkage to the variability of the crossover classes may be tested by comparing the standard deviation of two closely related progenies in one of which there is no linkage.

In lines 1 and 2 the standard deviation of the percentage of crossover classes in 21 ears with no linkage is to be compared with the standard deviation of the percentage of crossing over in 19 ears of the same parentage showing linkage. The variability of the linked group is greater by 4.85±0.53 per cent, a difference that is more than five times the probable error. The standard deviation of the percentage of crossing over in the ears with linkage also exceeds the standard deviation of the percentage of waxy by 3.5 times the probable error.

In lines 5 and 6 combined, where there was linkage, the standard deviation of the percentage of crossing over is 3.99±0.21. This is to be compared with the percentage of crossover classes in lines 7 and 8 where there is no linkage, 2.85±0.21. The difference of 1.14±0.3 is 3.8 times the probable error. It would appear that linkage increases the variability of the crossover classes.

Evidence has been presented in preceding paragraphs showing the ratio of crossovers to be more variable than the Mendelian ratios. Five of the groups of ears presented in Table 15 afford an opportunity to make a similar comparison when there is no linkage. If the greater variability of the percentage of crossing over is due to linkage, this increased variability should disappear when there is no linkage. The comparisons are presented in Table 16.

TABLE 16.—*Comparison of the standard deviations (σ) of the percentage of waxy seeds with those of the crossover classes where no linkage is operative*

Entry No. in Table 15—	Standard deviations (per cent)			D/E
	Per cent waxy seeds	Per cent crossovers	Crossovers—waxy	
1	2.45±0.26	1.81±0.19	−0.64±0.32	2.0
3	3.56± .37	3.58± .37	.02± .52	.4
4	2.30± .18	3.81± .30	1.51± .35	4.3
7	2.41± .26	3.14± .34	.73± .28	2.6
8	2.14± .21	2.58± .26	.44± .33	1.3

Entry No. 4 is outstanding and indicates the existence of factors operating on certain zygotic combinations. It should be noted that this entry covers a group of self-pollinated ears, homozygous dominant for the linked factor *C* and heterozygous for the *R* aleurone factor. None of the other differences are significant, and the array of differences weighted by the reciprocal of the probable error squared is 0.47±0.27.

It may be concluded that the differential death rate of zygotic combinations is not an important factor in the variability of the crossover classes.

VARIABILITY OF RATE OF CROSSING OVER ALIKE IN PLANTS HETEROZYGOUS AND HOMOZYGOUS DOMINANT FOR R

Four progenies are available in which half of the plants were heterozygous for the *R* aleurone factor, the other half being homozygous dominant for this factor. The factorial relations of these progenies are considered in detail on page 31 in connection with the rate of crossing over. These progenies provide an opportunity to determine whether the crossover rate is more variable when the *R* factor is heterozygous than when it is homozygous dominant. Eight comparisons are possible, involving measurements of male and female gametes separately and combined, the latter being selfed ears. The data are shown in Table 17.

The comparisons are made with σ_{50}, since the mean rate of crossing over was not alike in the two factorial groups. Table 17 shows that in no single comparison is there a significantly greater variability for one factorial composition as compared with the other. Combining the differences between the σ_{50} for the eight groupings shows that the plants heterozygous for *R* are on the average 0.53±0.24 per cent more variable than those homozygous dominant for this character.

The actual difference in variability is somewhat greater than the calculations show, since among the back-crossed ears listed as *R R*

there must be a few which in reality were heterozygous for *R* in one parent. Since plants heterozygous for *R* have a somewhat lower rate of crossing over than those homozygous dominant for this factor, the standard deviations for the *R R* group are too high. No adequate estimate of the number of such ears can be made, but it is doubtful whether enough such cases exist to destroy a significant difference. It may be concluded, therefore, that the *R* factor in heterozygous conditions is not associated with a greater variability in rate of crossing over between *C* and *Wx*.

TABLE 17.—*Comparison of the variability of crossover rate between C and Wx in plants homozygous and heterozygous for the R aleurone factor*

Progeny	Heterozygous sex	Variability (σ_{50}) of crossover rate (per cent)		Difference (*R R*−*R r*)	*D*/*E*
		R R	*R r*		
Dh 416L3L1C5L3L1R23	Female	6.41±0.48	5.94±0.56	0.47±0.73	0.64
	Male	5.44± .33	6.07± .39	− .63± .51	1.23
	Female and male	6.50±1.03	5.50± .79	1.00±1.30	.77
Dh 416L3L1C5L3L2R23	Female	6.90±1.10	7.34± .94	− .44±1.44	.31
	Male	5.61±1.20	7.85±1.32	−2.24±1.78	1.26
	Female and male	5.31±1.03	8.33±1.78	−3.02±2.05	1.47
Ph 230L1 and L2R24	Female	5.77± .61	7.53± .67	−1.76± .91	1.93
	Male	9.05± .94	9.19±1.13	− .14±1.47	.10
Mean				− .53± .24	2.19

RATE OF CROSSING OVER BETWEEN THE C–Wx GENES

With the linked genes *C*–*Wx*, crossover rates ranging from 8 to 50 per cent have been found in sibs of inbred progenies. In these cases the number of seeds precluded the possibility of their being chance departures from a common mean. The situation with respect to a moderately variable progeny is presented graphically in Figure 1.

Before a definite arrangement of the many characters of the mature plant could be attempted it seemed necessary to gain an insight into the factors that were causing the great differences between progenies and individuals, in the closeness of the linkage of the aleurone gene *C* and the endosperm gene *Wx*. It was first thought that the differences were due to heritable mutations in the rate of crossing over, and as a first step in the demonstration of the correctness of this hypothesis progenies were grown from ears of widely different degrees of linkage. The results were disappointing, in that the hypothesis was both supported and contradicted by the evidence.

At the present time (now seven generations from the first hybrid generation) there is conclusive evidence that a strain has been isolated which will give with some consistency 35 to 39 per cent of crossing over between *C* and *Wx*, while another strain for which the evidence is not so conclusive will give from 17 to 22 per cent of crossing over between these factors.

Many more progenies having crossover percentages at all points between these two centers have been obtained, but nothing can be stated as to the stability of these intermediate positions.

Although the best evidence now available indicates that heritable differences are involved in the variable percentages of crossing over, this conclusion has not been reached without many discordant facts and clear evidence that factors other than heritable ones also affect the rate of crossing over. In an effort to establish high and low rates of crossing over by growing representatives of the extremes, it was found that inheritance of the parental condition is the exception rather than the rule and that most of our progenies show complete regression to the mean of the parental progeny. Occasionally also the offspring of extreme parents show crossover percentages at the opposite end of the scale, in consequence of which it has been concluded that environmental factors sometimes obscure the true genetic condition.

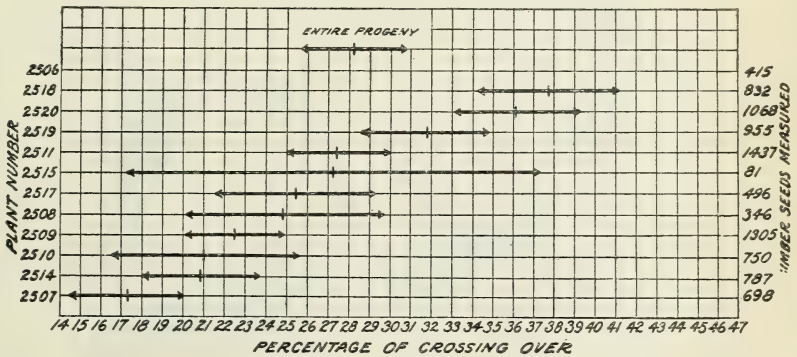

FIG. 1.—The percentage of crossing over in the male gametes of individual plants of Dh 416L3L1C1L2L23 plotted with a range of ± three times the probable error. The short vertical lines indicate the percentage of crossing over

The behavior of the crossover ratio of four closely related progenies over a period of several generations is shown graphically in Figures 2, 3, and 4.

Both selfed and back-crossed ears are included. The selfed ears are located at the observed rate. The observed rate in back-crossed ears was corrected for difference in sex by taking the geometric mean of the observed rate and the mean rate of the opposite sex for the progeny.

The figures in the body of the diagram show the number of ears having the percentage of crossing over indicated by the position of the figure in each instance.

All progenies are the result either of selfing or of back crosses with sibs.

CROSSING OVER GREATER IN SOME PROGENIES THAN IN OTHERS

Attempts have been made to arrive at a single expression for the distance separating two linked genes on the chromosome. In the light of the data accumulated for the *C–Wx* genes such efforts

would appear to be futile. With only 14 progenies, all closely related, the rate of crossing over ranges from 17 to 38. Individual plants with significantly lower and higher rates have appeared, and there seems little reason to doubt that progenies having still lower or higher rates could be obtained. With Mendelian ratios the interaction of a definite number of genes makes possible an expected ratio from which departures may be calculated, but with the crossover ratio there is no fixed point of departure. The best that can be expected is to determine the rate under constant environmental conditions and a particular genetic complex. Once determined, there is no reason—in maize at least—for assuming the particular complex of genetic and environmental factors to be typical.

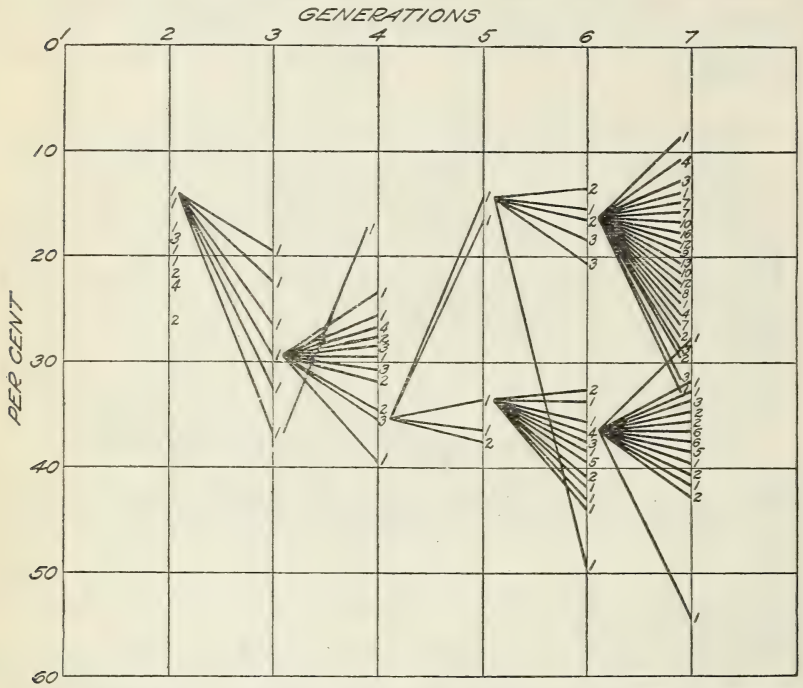

FIG. 2.—Inheritance of percentage of crossing over, showing isolation in the fifth generation of two strains having widely different mean crossover rates

Stadler (*16*), working with three families, has shown that the mean rate of crossing over between *C* and *Wx* is not alike in the three strains. From a comparison of the differences between ears borne on the same plant, he concludes that variations in degree of linkage are due at least in part to environmental factors.

In stability, the rate of crossing over does not approach that of the proportions of the Mendelian characters, and there would seem to be no justification for assuming a definite fixed rate of crossing over between pairs of linked genes.

The situation with respect to the *C–Wx* linkage is shown graphically for 16 progenies in Figure 5 and the biometrical constants are given in Table 5 (p. 12).

PROPORTION OF CROSSOVER TO NONCROSSOVER GAMETES NOT AFFECTED BY VITALITY OF POLLEN

Early experiments indicated that crossing over in the male gametes was more variable than in the female. Since the male flowers are more exposed than the female, the male gametes are subjected to greater vicissitudes. The seasonal and climatic factors, therefore, might be expected to influence the rate of crossing over or to act as a selecting agency on the gametes after they were formed.

Preliminary analysis of linkage data amassed for other purposes showed a rather high positive correlation between the number of seeds on an ear and the percentage of crossing over, when the pollinations were so made that the seed-bearing parent was homozygous recessive for the characters in question. This correlation seemed best explained as resulting from a death rate of the crossover classes

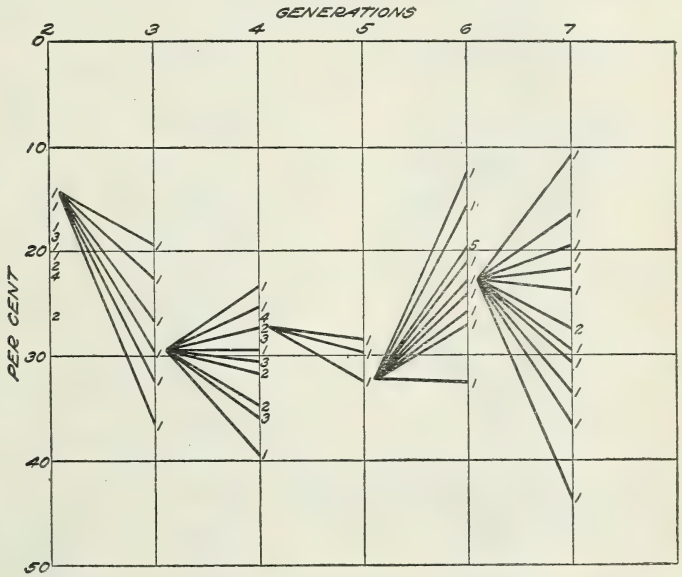

FIG. 3.—Inheritance of percentage of crossing over, showing the ancestry of a strain having an extremely variable rate of crossing over, the variability increasing with the progress of generations

in the male gametes. Subsequent material of a more homogeneous nature has failed to substantiate the magnitude of the correlation between fertility and crossing over, but before these additional data were available it seemed desirable to test directly the effect of unfavorable conditions on the percentage of crossing over in the male gametes.

The simplest plan and one in harmony with natural conditions seemed to be to apply fresh heterozygous pollen to the double-recessive parent, store the remainder, and apply it at different periods throughout the day. Accordingly two heterozygous plants were selected, and on several days samples of pollen collected from them in the morning were applied at various times. For a variety of reasons these preliminary investigations were not conclusive, but demonstrated a decreasing viability of pollen with the increase in time of storage, showing that the opportunity for selective action

was present. It was found that the viability of pollen collected at 9 in the morning was reduced about 50 per cent by being stored for 7 hours.

The following season a more extensive program was undertaken involving 40 heterozygous plants, but the short-interval pollinations were eliminated, the whole effort being placed on a 7-hour period of storage.

In practice it was found convenient to collect the pollen, make one application of half the total quantity (anther free), and then attach the bag containing the remainder to the plant which had been selected for pollination 7 hours later.

Several methods of measuring the quantity of pollen used were tried, but as none were satisfactory this refinement was discarded and an attempt made to divide the anther-free pollen into two visibly equal lots. From the numerous double applications only 13 pairs of ears were obtained, many failing on one side or the other. The pertinent facts with respect to these ears are shown in Table 18.

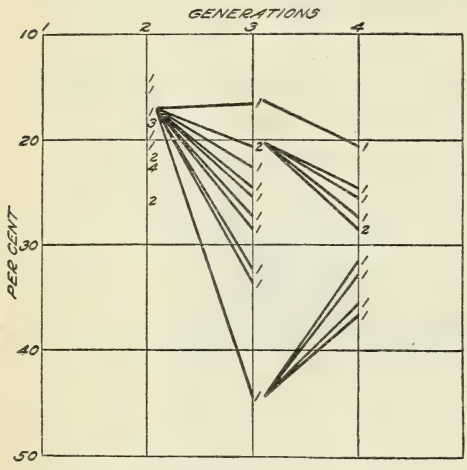

FIG. 4.—Inheritance of percentage of crossing over, showing progenies of extreme rates regressing toward the mean of the parental progeny

The immediate interest was in the percentage of crossing over, and, as the table shows, there is little difference in the percentage of crossing over between fresh and old pollen, though the average storage period is 7 hours and 14 minutes and the indicated death rate is 35 per cent.

Although the survival of crossover gametes does not seem to be affected by the factors which brought about the loss of viability, there is striking evidence that the percentage of pollen grains bearing the waxy character has been greatly increased.

The data leave no room to doubt that a profound alteration in the proportion of waxy to horny pollen grains has taken place. Similarly, though not to the same degree, the proportion of white-carrying to color-carrying gametes has been altered by the storage of pollen. Analysis of the data, however, shows that the increased proportion of white to colored is simply a dependent result of the increase in the percentage of viable waxy pollen due to the correlation between waxy and white.

Although in pollen stored for seven hours the increase in the percentage of waxy seeds over the expected equality is most striking, the fact must not be overlooked that the proportion of waxy seeds resulting from the application of fresh pollen is below equality by a percentage too large to be attributed to chance. The point is important, as it indicates that a simple differential death rate for the two sorts of pollen will not account for the observed results. From

the evidence it would seem logical to conclude that a differential maturity is involved, with the waxy pollen reaching maturity at a later period than the horny.

TABLE 18.—*Differences in percentages of white, waxy, and crossovers, in fresh and old pollen of back-crossed ears* (♀ *cc wx wx* × ♂ *Cc Wx wx*)

[The minus sign preceding a difference indicates cases where the old pollen was deficient]

Heterozygous plant No.	Age of pollen		Pollen application	Number of seeds	Percentage of—		
	Hr.	Min.			White	Waxy	Crossovers
3988	8		Fresh	824	46.1±1.17	45.5±1.17	33.3±1.11
			Old	148	64.2±2.65	76.4±2.35	34.0±2.62
			Difference		18.1±2.88	30.9±2.61	.7±2.84
3984	8	10	Fresh	577	50.4±1.40	44.0±1.92	38.8±1.37
			Old	289	57.8±1.95	80.3±1.58	33.5±1.87
			Difference		7.4±2.41	36.3±2.49	−5.3±2.32
3993	7	40	Fresh	496	47.8±1.51	48.0±1.51	37.0±1.46
			Old	233	54.5±2.20	63.9±2.12	41.3±2.17
			Difference		6.7±2.67	15.9±2.62	4.3±2.62
3989	7	15	Fresh	295	42.7±1.94	44.1±1.94	39.9±1.92
			Old	69	52.2±4.05	56.5±4.03	39.2±3.98
			Difference		9.5±4.63	12.4±4.46	−.7±4.41
3994	7	10	Fresh	359	47.7±1.78	45.1±1.77	41.1±1.75
			Old	257	52.9±2.10	60.7±2.05	34.0±1.99
			Difference		5.2±2.75	15.6±2.72	−7.1±2.65
4009	7		Fresh	160	47.5±2.66	43.8±2.64	47.7±2.67
			Old	133	57.9±2.88	82.0±2.25	46.5±2.92
			Difference		10.4±4.00	38.2±3.47	−1.2±3.95
4010	8	05	Fresh	355	50.7±1.79	48.7±3.18	43.7±1.78
			Old	371	55.5±1.74	61.5±1.70	40.6±1.72
			Difference		4.8±2.49	12.8±2.17	−3.1±2.47
3998	8	20	Fresh	628	44.7±1.34	43.0±1.33	35.6±1.29
			Old	674	49.4±1.30	53.9±1.29	33.0±1.23
			Difference		4.7±1.87	10.9±1.85	−2.6±1.78
3977	5	25	Fresh	181	53.0±2.50	55.2±2.48	36.5±2.41
			Old	128	53.1±2.98	52.3±2.98	38.3±2.91
			Difference		.1±3.77	−2.9±3.86	1.8±3.77
4013	7		Fresh	283	48.1±2.00	46.3±2.00	33.5±1.88
			Old	313	57.8±1.88	76.0±1.63	39.9±1.87
			Difference		9.7±2.75	29.7±2.58	6.4±2.65
4019	8	20	Fresh	408	50.0±1.67	44.9±1.66	34.9±1.59
			Old	77	67.5±3.60	62.3±3.70	33.0±3.63
			Difference		17.5±3.97	17.4±4.07	−1.9±3.95
4022	7	30	Fresh	[1] 974	48.2±1.08	46.9±1.08	38.1±1.05
			Old	635	50.1±1.34	51.6±1.34	37.2±1.29
			Difference		1.9±1.72	4.7±1.72	−.9±1.66
3992	5	25	Fresh	310	52.9±1.91	47.4±1.91	38.8±1.87
			Old	26	53.8±6.66	38.5±6.44	36.4±6.36
			Difference		.9±6.94	−8.9±6.72	−2.4±6.60
Total			Fresh	5,850			
			Old	3,353			
Mean			Fresh	400	48.1 ± .48	45.98± .44	37.55±.61
			Old	258	53.98± .83	62.03±2.00	36.91±.67
			Difference		6.50±.676	16.73±2.2	−1.18±6.59

[1] Average of three fresh (a. m.) pollinations.

Although this assumption would account for the long-observed deficiency of waxy seeds in heterozygous material provided the pollinations were made early, the actual facts with respect to our material are quite otherwise. For years it has been customary to make all pollinations in the afternoon, in the belief that most pollen was shed in the early morning and was well out of the air at the time pollinations were made. It is difficult to reconcile the results of our regular practice with the facts disclosed by this age-of-pollen experiment, and further investigation is essential to gain enlightenment on these matters.

From the standpoint of methods of measuring crossing over, it is of interest to observe that with such widely aberrant Mendelian ratios as are obtained with old pollen Yule's coefficient of association (Q) provides a satisfactory index of the gametic proportions.

Brink (*4*) has found that in material involving the I aleurone factor the ratio of waxy to nonwaxy seeds is modified in some manner by this factor. His conclusions as to the effect of this factor are based on the following procedure:

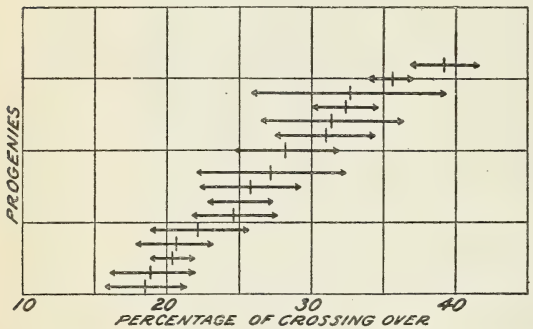

FIG. 5.—Percentage of crossovers in female gametes of 16 closely related progenies arranged in an ascending series of mean crossover percentages and plotted with a range of ± three times the probable error of the progeny means. The mean is indicated for each progeny by a short vertical line

> The four classes of seeds from an ear segregating for white and waxy and known to have resulted from the combination *IWx iwx* × *iwx iwx* were planted separately and crosses made between the combinations *I i Wx wx* × *i i wx wx* and *I i wx wx* × *i i Wx wx*.

It was found that crosses of the former sort gave an excess of waxy seeds which in some instances reached 63 per cent waxy, and the latter combination gave a deficiency. Brink noted further that the increased number of waxy seeds was largely confined to the *i i wx wx* zygotes.

Since *I* and *W x* were linked, an excess of waxy zygotes would be made up largely of the class *i i wx wx*, and in the absence of the detailed figures it is possible that Brink's excess of this combination is due to the linkage of these genes. With this interpretation, his results agree with ours where an excess of waxy seeds, brought about through devitalized pollen, was accompanied by an increase in the percentage of white seeds. If this were not the case, the linkage relations of *I* and *Wx* would be modified profoundly in those cases where an excess of waxy seeds occurred.

With our material involving the *C* factor (a gene closely linked with *I*) there is no evidence that the nature of this factor has any effect on the ratio of waxy to nonwaxy seeds. Thus the ears shown in Table 18 are made up of the combination *c c wx wx* × *C c Wx wx*, a combination that corresponds to Brink's case where an excess of waxy seeds was found. Our results show that when fresh pollen is used there is a significant deficiency of waxy seeds, though if the

pollen is stored for several hours an excess of waxy seeds results. The second combination *C c wx wx* × *c c Wx wx*, which corresponds to Brink's case where a deficiency of waxy seeds was found, is shown in Table 19. Obviously there is no difference between the percentage of waxy seeds obtained with this combination and that obtained when the noncrossover combination was used, the percentage found in the former case (Table 18) being 45.98±0.44 and in the latter (Table 19) 45.96±0.27.

Further evidence on this point is found in summarized form in Table 15, an inspection of which shows that the percentage of waxy seeds is not affected by the nature of the aleurone factors *C* and *R* when the percentages of waxy in entries 3 and 4 are compared with those in entries 1 and 2, nor by the nature of the cross, that is, whether between crossover or noncrossover classes when the percentage of waxy in entry 5 is compared with entry 7 and entry 6 compared with entry 8.

TABLE 19.—*Reciprocal crosses of colored waxy (C c wx wx) × white horny (c c Wx wx)*

Reciprocal cross	White horny, female			Colored waxy, female		
	Number of seeds	Percentage of white	Percentage of waxy	Number of seeds	Percentage of white	Percentage of waxy
3882×3776	290	46.6±1.98	53.1±1.98	189	47.1±2.45	47.1±2.45
3885×3787	180	53.9±2.50	41.7±2.47	198	57.6±2.37	48.5±2.39
3888×3778	515	49.1±1.48	48.0±1.48	538	44.8±1.45	45.0±1.45
3892×3784	150	51.3±2.75	44.0±2.72	72	54.2±3.96	43.1±4.27
3895×3787-2	61	41.0±4.24	57.4±4.26	589	51.3±1.39	45.8±1.38
3898×3793	97	46.4±3.41	48.4±3.42	26	53.8±6.58	38.5±6.42
3900×3789	414	47.6±1.65	51.7±1.65	510	45.1±1.49	47.6±1.49
3907×3802	592	45.3±1.38	49.5±1.38	445	46.5±1.59	46.1±1.59
3907-2×3801	224	50.0±2.25	54.0±2.24	450	52.2±1.58	43.1±1.57
3909×3804	447	45.9±1.59	48.5±1.59	628	47.1±1.34	45.5±1.34
3916×3808	505	51.5±1.50	51.7±1.50	416	49.8±1.65	46.9±1.64
3916-2×3808-2	585	48.4±1.39	50.1±1.39	360	50.3±1.77	46.4±1.77
3919×3806	438	47.3±1.60	48.4±1.60	550	49.4±1.44	45.6±1.43
3922×3803	419	50.8±1.64	50.4±1.64	256	45.7±2.08	48.4±2.10
Mean		48.34± .44	49.75± .48		48.67± .56	45.96± .27

CROSSING OVER REDUCED BY THE R ALEURONE FACTOR IN A HETEROZYGOUS CONDITION

In 1921 aberrant color ratios appeared in a progeny of the cross Dh 416. This progeny was one of many that had been grown since the original cross was made in 1914, all being heterozygous for the *C* aleurone factor. The following season it was determined that the irregularities were due to another factor for aleurone color complementary to *C* and located in another chromosome. It now has been demonstrated that this is the factor *R*, which must have mutated from the dominant to the recessive condition. The bearing of this on the present study is that in two of the progenies used in studying the linkage relations of *C* and *Wx* there were plants heterozygous for *R*, giving back-crossed ears with 62.5 per cent white and selfed ears with 43.75 per cent white. The event has proved fortunate, since it has resulted in a demonstration that the presence of *R* in a heterozygous condition is associated with a lower crossing over between *C* and *Wx*.

Hutchison (*9*) found that crossing over in *C–Sh–Wx* stock was approximately 80 per cent of that in an *I–Sh–Wx* stock and suggested that a crossover modifier might be responsible. The lower rate of crossing over applied equally to both regions of the chromosome. The factors *I* and *C* are very closely linked, and the apparent distance between *I* and *Wx* was found to be 26.18 units and that between *C* and *Wx* was but 21.88 units. The difference between the two stocks is no greater than that found between many of our progenies where the *I* factor is not involved and may represent merely progeny difference rather than the effect of a crossover modifier, but the point is of interest in view of the effect of the *R* factor.

From the two progenies which contained plants that were heterozygous for *R*, crossing over was measured in 140 individuals. These fall into six groups, the reciprocal back crosses and the selfed ears from each of the two progenies. In Table 20 the rate of crossing over in the individuals that are homozygous for *R* in each of these six groups is compared with the rate in those heterozygous for *R*.

TABLE 20.—*Comparison of the percentage of crossing over in plants homozygous for the R aleurone factor with those heterozygous for this factor*

Nature of cross	Homozygous for *R*			Heterozygous for *R*			Crossover difference	
	Number of ears	Number of seeds	Percentage of crossovers	Number of ears	Number of seeds	Percentage of crossovers	*R R*−*R r*	*D/E*
Dh 416L3L1C5L3L1R23								
Back crosses:								
Female heterozygous	41	19,759	20.77±0.54	26	14,258	20.19±0.61	0.58±0.82	0.7
Male heterozygous	60	27,725	19.14± .37	56	24,202	16.97± .41	2.17± .55	3.9
Self	9	4,455	21.48±1.10	11	3,156	19.12± .82	2.36±1.37	1.7
Dh 416L3L1C5L3L2R23								
Back crosses:								
Female heterozygous	9	4,710	24.34±1.79	14	6,763	21.20±1.17	3.14±1.72	1.8
Male heterozygous	5	2,225	27.18±1.52	8	2,588	25.44±1.63	1.74±2.23	.8
Self	6	2,032	23.77±1.25	5	1,477	24.80±2.17	−1.03±2.50	.4
Mean							1.75±0.28	6.2

The differences between the mean crossing over of plants with *R R* and *R r* in the six groups, when treated as a population weighted by the reciprocal of the squared probable errors, show a mean percentage of 1.75±0.28, a departure from zero of more than six times the probable error. Five of the six determinations are positive in sign, the group with the smallest number of ears being the only exception.

Plants with heterozygous *R* were identified by the resulting ratio of white to colored seeds. In back-crossed ears there are three combinations that would give 50 per cent white:

$$\frac{c\ R\ wx}{C\ R\ Wx}\times\frac{c\ R\ wx}{c\ R\ wx},\ \frac{c\ R\ wx}{C\ R\ Wx}\times\frac{c\ r\ wx}{c\ R\ wx},\ \text{and}\ \frac{c\ r\ wx}{C\ R\ Wx}\times\frac{c\ R\ wx}{c\ R\ wx}.$$

This made it impossible to detect all of the double heterozygous plants that were also heterozygous for *R*. There were, however, nine plants in the back-crossed group of the first progeny giving 50 per cent white, which by other pollinations were shown to be heterozygous

for *R*. This group, although giving 50 per cent white, had a crossing over of 16.90±0.805, which agrees well with 16.97, the average of the group heterozygous for *R*, and differs from the average of the group with homozygous *R* by 2.5 times the probable error. Besides supporting the results from the group with 43.75 per cent white, these results indicate that the differences are not due to the method of measuring the crossing over when one of the characters is dihybrid.

Among the plants heterozygous for *R* back crossed on more than one individual, there were seven that were used both on plants homozygous dominant for *R*, resulting in 50 per cent white seeds, and plants heterozygous for *R*, giving 62.5 per cent white seeds. If the lower crossing over of the plants segregating 62.5 per cent ascribed to the heterozygous *R* was due to the method of measuring the crossover, a comparison of the two rates in these seven plants should disclose the fact. The data are presented in Table 21.

The results show no consistent differences between the rate measured when 50 per cent of the seeds are white and that with 62.5 per cent white.

TABLE 21.—*Percentage of crossing over in the male gametes of individuals back crossed on plants homozygous for R compared with the crossing over in the same individuals when back crossed on plants heterozygous for R*

Male parent	Female parent				Difference (*R R*−*R r*)
	c c R R wx wx		*c c R r wx wx*		
Cc Rr Wx wx	Number of seeds	Percentage of crossovers	Number of seeds	Percentage of crossovers	
Plant No. 5901	1,523	14.2	1,157	14.3	−0.1 ±0.9
Plant No. 5905	379	26.1	1,229	23.4	2.7 ±1.7
Plant No. 5955	2,471	19.9	328	13.8	6.1 ±1.4
Plant No. 5976	324	17.0	526	22.6	−5.6 ±1.9
Plant No. 5911	170	12.9	229	5.2	7.7 ±2.0
Plant No. 5918	636	16.9	264	22.3	−5.4 ±2.0
Plant No. 5909	510	16.0	713	15.4	.6 ±1.4
Mean					.96± .99

It follows that the reduction of crossing over associated with heterozygous *R* probably is somewhat larger than our results indicate, for there is no way of detecting all of the individuals heterozygous for *R* in the groups giving 50 per cent white.

In the second progeny the number of plants is much smaller, and in none of the groups taken individually are there significant differences between the plants with *R R* and *R r*, but since none of the groups departs significantly from the corresponding group in the first progeny, they are combined in the table. In this second progeny, which was the result of selfing a plant of the gametic composition $\frac{C\ R\ Wx}{c\ r\ wx}$, there were four ears with the linkage between dominant and recessive, one back-crossed ear giving 25 per cent white ($C\ c\ R\ R\ Wx\ wx \times C\ c\ r\ r\ wx\ wx$) and three back-crossed ears with 75

per cent white ($C\ c\ R\ r\ Wx\ wx \times c\ c\ r\ r\ wx\ wx$). It can not be shown that the crossing over in any of these classes is not a chance departure from that of the larger groups, and they are therefore included in the table. If they are excluded, however, and the comparison confined to the back-crossed ears giving 50 per cent and 62.5 per cent white, the individual comparisons become statistically significant.

That the association between heterozygous R and a reduced crossing over is not peculiar to this hybrid is shown by the results from another distantly related hybrid, Ph 230, considered later in connection with the factor for sweet seeds.

The mean crossing over in the several groups is shown in Table 22. In this progeny the effect of heterozygous R appears to be confined to the formation of the female gametes. The difference between the mean of the 20 back-crossed ears with homozygous R and that of the 33 ears with heterozygous R is 4.15±0.96 per cent, a difference of more than four times the probable error.

TABLE 22.—*Crossover values in the several gametic groupings of the hybrid Ph 23OL1 and L2R24*

Nature of cross	Gametic composition	Number of ears	Number of seeds	Percentage of crossovers
Female heterozygous:				
50 per cent white	$\left\{ \frac{c\ R\ wx}{C\ R\ Wx} \times \frac{c\ r\ wx}{c\ r\ wx} \right\}$	20	10,374	21.59±0.69
62.5 per cent white	$\left\{ \frac{c\ r\ wx}{C\ R\ Wx} \times \frac{c\ r\ wx}{c\ R\ wx} \right\}$	29	9,933	17.70± .70
Do	$\left\{ \frac{c\ r\ wx}{C\ R\ Wx} \times \frac{c\ r\ wx}{C\ r\ wx} \right\}$	4	1,285	15.46±2.35
75 per cent white	$\left\{ \frac{c\ r\ wx}{C\ R\ Wx} \times \frac{c\ r\ wx}{c\ r\ wx} \right\}$	16	5,641	21.88±1.03
Male heterozygous:				
50 per cent white	$\left\{ \frac{c\ r\ wx}{c\ r\ wx} \times \frac{c\ R\ wx}{C\ R\ Wx} \right\}$	21	5,883	26.19±1.16
62.5 per cent white	$\left\{ \frac{c\ r\ wx}{c\ R\ wx} \times \frac{c\ r\ wx}{C\ R\ Wx} \right\}$	15	5,654	26.73± .84

In this hybrid it is evident also that the crossing over in the group giving 75 per cent white is not reduced, although R is heterozygous. There were 16 ears of this character with 5,641 seeds and a mean crossover of 21.88±1.03 per cent. This might be explained by assuming that to reduce the crossing over the heterozygous R must enter from both parents. But if this were true the group of back-crossed ears resulting from the combination $C\ c\ R\ r\ Wx\ wx \times C\ c\ r\ r\ wx\ wx$ should have a high rate of crossing over. Ears of this character can be detected by the low value of Q, which can only reach 0.5 with perfect linkage. Because of the linkage between C and Wx this combination is relatively rare, but there were 4 among the 33 back-crossed ears giving 62.5 per cent white, and their mean crossover percentage is only 15.46±2.35, a rate even lower than that of the group to which they have been assigned. The small number of ears, however, makes the probable error so large as to leave open the possibility that they are a chance departure from the $R\ R$ group. The difference is 6.14±2.45 per cent.

It should be noted also that in this hybrid the crossing over is lower in the female. It agrees in this respect with the second progeny of Dh 416 and suggests the idea that the effect of heterozygous *R* may be apparent only when the crossing over is low.

It is obvious that the effect of heterozygous *R* is influenced by the nature of the gametic composition and that the apparent differences are reduced by combining all classes, as has been done in Table 22. With the present data, however, it seems unwise to go farther than to conclude that heterozygous *R* is associated with a reduced crossing over.

Additional evidence is to be found in the published data of Kempton (*11 pp. 71–73*). His tables give the correlation between *C* and *Wx* in two groups of ears, one homozygous for *R* and the other with *R* heterozygous. The *R R* group has 20 ears with 12,394 seeds and a mean crossing over of 24.9±0.33 per cent. The *R r* group has 4 ears with 2,477 seeds and a mean crossing over of 23.3±0.40 per cent. The difference is 1.6±0.52 per cent, a little more than three times its probable error.

RATE OF CROSSING OVER BETWEEN C AND Wx ASSOCIATED WITH THE Su FACTOR

In view of the fact that the rate of crossing over between *C* and *Wx* is reduced when the aleurone factor (*R*) not in the chromosome with the linked pair is in a heterozygous condition, it becomes of interest to test the effect of other factors not involved in the production of color.

Material was available involving the factor for sweet endosperm *Su*. The hybrid furnishing this material had as one parent a strain of the Dh 416 cross used throughout the present study, but the parent providing the sweet endosperm was from an entirely unrelated variety. The Dh 416 parent with respect to the factors under discussion was constituted *C C R R wx wx Su Su*, and the sweet parent had the gametic constitution of *c c r r Wx Wx su su*.

Crossed seed was colored horny, and the F_1 plants when self-pollinated had colored and white seeds in the ratio of 9 to 7. With respect to the texture of the endosperm the seeds were classed as 9 horny, 3 sweet, 3 waxy, and 1 waxy-sweet. Colored-horny and white-waxy seeds were planted and back-crosses obtained between them after the homozygous horny plants had been eliminated by means of pollen tests.

The complicated aleurone and endosperm condition necessitates subdividing the data to differentiate the several types of ratios, and the data are considered further from the standpoint of sex.

The ears composing these several groups are found in Table 23. Since the primary consideration is to test the effect of heterozygous *Su* as compared with homozygous *Su*, each aleurone group is divided into two classes on the basis of whether or not sweet seeds were produced. Since all the ears tested are the result of back crosses on white-waxy plants that were either heterozygous or homozygous for *Su*, it is not possible to identify the ears in the nonsweet group that were heterozygous for *Su* in one parent but were fertilized with pollen from a plant homozygous for *Su*. A certain proportion of the ears having no sweet seeds in one parent or the other, therefore, were heterozygous for *Su*. With this limitation in mind, the tables

may be examined for the effect of the *Su* factor. It will be seen that in none of the comparisons is the difference statistically significant. It should be noted, however, that in three comparisons where the female is the heterozygous parent there is a higher crossing over in the ears not segregating for *Su*.

TABLE 23.—*Comparison of percentages of crossing over in plants heterozygous for Su with those in plants homozygous dominant for this factor*

Nature of cross	Heterozygous for *Su*			Homozygous for *Su*			Difference (homozygous—heterozygous)	*D/E*
	Number of ears	Number of seeds	Percentage of crossovers	Number of ears	Number of seeds	Percentage of crossovers		
Female gametes:								
50 per cent white	10	5,637	21.21±1.20	10	4,737	22.04±0.57	0.83±1.33	0.62
62.5 white	12	4,576	16.19±1.18	22	6,642	18.31±.76	2.12±1.40	1.52
75.0 per cent white	11	4,426	20.61±1.14	5	1,215	26.49±1.63	5.88±1.99	2.95
Male gametes:								
50.0 per cent white	9	2,451	26.99±2.30	12	3,432	25.62±.95	−1.37±2.47	.55
62.5 per cent white	5	1,873	27.72±1.54	10	3,781	26.24±.98	−1.48±1.79	.83

RATE OF CROSSING OVER DIFFERS IN THE TWO SEXES

One of the most striking facts concerning the association of the chromosomes with the transmission of characters is that in many forms the chromosomes behave very differently in the formation of male and female gametes. In the male of Drosophila when the segregation of characters takes place in the formation of gametes the chromosomes behave as units. All the characters of any given chromosome are transmitted together as they were received from the parents. It would seem not unreasonable that this difference should in some way result from cytological differences in the genesis of the microspores and megaspores, but there are other forms in which the reverse is true, and it is the female in which there is no crossing over. In still other forms, especially in many monœcious plants, there appears to be an equal degree of freedom of crossing over in the two sexes. So long as difference in rate of crossing over remains an isolated fact unrelated to other cytological or genetic phenomenon, it will be necessary to grope for bearings and approach the problem from as many angles as possible.

In Drosophila, where there is absolutely no crossing over in the male, it seems difficult to proceed by other than cytological methods, but in species where the crossing over takes place in both sexes but with different degrees of freedom it should be possible to determine at least some of the factors that influence or are associated with the diversity.

Individual diversity in the rate of crossing over is so great that little reliance can be placed on comparisons of the male and female rate of crossing over unless the rate in both sexes is measured in the same individuals. Furthermore, there is some evidence that the apparent rate of crossing over is influenced by the double recessive parent. For this reason the material examined in this connection has been restricted to reciprocal crosses of double-heterozygous and double-recessive individuals.

The records afford 13 progenies with from 4 to 49 reciprocal back crosses. The data are presented in detail in Table 24 and summarized in Table 25. The material includes 151 reciprocal crosses. Measurements of crossing over in the female involve 70,898 seeds, and the reciprocals measuring the crossing over in the male involve 71,391 seeds.

In 9 of the 13 progenies the crossing over was lower in the male and in 4 the crossing over was lower in the female. There is therefore little ground for assuming any general tendency. In 6 of the 9 progenies in which the male has the lower rate the difference is greater than three times the probable error, and in 2 the difference is more than six times the probable error. Thus there is no ground for explaining these differences as chance variations. It is equally obvious, however, that at least 3 of the 4 progenies in which the females have the lower rate are not chance departures from equality or from the general mean.

INDIVIDUAL VARIATIONS IN THE CROSSOVER DIFFERENCE

It is possible to go further and show that variations in the crossover differences of the individual plants of a progeny are not chance departures from the mean of the progeny. This is best exemplified in progeny shown in entry 10, Table 24, grown at Arlington, Va., in 1923. In this progeny, crossing over in the male and female gametes was measured in 49 individuals. Crossing over in the males averaged 2.78 per cent lower than in the females. The individual differences range from −13.6 to 14 and many depart from the mean to an extent that can not be ascribed to chance. Eight are more than four times the probable error, five are more than five times, and three are more than six times the error.

Although all progenies are rather closely related, it is of interest to examine their pedigrees for evidence of genetic factors affecting crossover difference. Entry 9, Table 25, with a significantly lower average crossing over in the female, is a back cross between two sister plants of entry 8, which showed a significantly lower average crossing over in the male, and the heterozygous plant parent of entry 9 had a lower crossing over in the male of 5.9 per cent. Entries 10 and 11 were from two ears on the same plant. No. 10 was pollinated by a sister plant from a white-waxy seed and No. 11 was selfed. The difference between these two progenies is nearly 10 times the probable error.

Thus there is no evidence that the pronounced diversity in the relative frequency of crossing over in the male and female is the result of genetic differences.

When we turn to possible environmental differences for an explanation of the diversity, the results are equally baffling. Entries 10 and 11 that differ so profoundly were grown in adjacent rows and flowered simultaneously.

Emerson and Hutchison (*6*) have reviewed the literature of crossing over in the two sexes in plants and report experiments with two pairs of linked factors in maize.

TABLE 24.—*Comparison of the rate of crossing over in male and female gametes of plant reciprocals, with summary of seed classes for the individual ears*

Entry No., progeny designation, and reciprocals	Female parent heterozygous						Male parent heterozygous						Difference (female − male)
	Number of seeds					Per cent-age of cross-overs	Number of seeds					Per cent-age of cross-overs	
	Phenotypic classes				Total		Phenotypic classes				Total		
	C Wx	*C wx*	*c Wx*	*c wx*			*C Wx*	*C wx*	*c Wx*	*c wx*			
(1) Dh 416L3L1C1L1L22:													
2447×2428	246	83	86	210	625	27.0	176	62	48	182	468	23.5	3.5
2452×2431	73	20	19	80	192	20.3	120	28	25	101	274	19.3	1.0
2455×2437	213	85	76	224	598	26.9	149	46	45	185	425	21.4	5.5
2459×2439	203	60	46	195	504	21.0	289	63	70	296	718	18.5	2.5
Total or mean					1,919	24.75					1,885	20.53	3.34±0.50
(2) Dh 416L3L1C1L1L1L23:													
2474×2443	159	66	67	146	438	30.4	104	62	63	90	319	39.2	−8.8
2477×2445	367	107	94	368	936	21.4	14	2	3	20	39	12.8	8.6
2465×2447	233	73	95	226	627	26.8	122	27	30	117	296	19.3	7.5
2468×2450	134	27	24	118	303	16.8	39	10	10	33	92	21.7	−4.9
2471×2452	94	51	46	100	291	33.3	137	41	40	140	358	22.6	10.7
2473×2455	141	56	58	149	404	28.2	221	81	53	208	563	23.8	4.4
2463×2457	150	63	50	138	401	28.2	177	50	43	167	437	21.3	6.9
Total or mean					3,400	25.80					2,104	24.50	3.42±1.66
(3) Dh 416L3L1C1L1L2L23:													
2506×2485	108	92	74	93	367	45.2	133	88	88	106	415	42.4	2.8
2508×2484	103	16	22	91	232	16.4	137	41	45	123	346	24.9	−8.5
2511×2484	170	68	66	150	454	29.5	81	32	33	80	226	28.7	.8
2515×2491	49	24	19	58	150	28.7	24	14	8	35	81	27.2	1.5
2517−2×2482	132	64	42	124	362	29.3	196	68	58	174	496	25.4	3.9
2518×4645	162	107	85	194	548	35.0	155	96	90	168	509	36.5	−1.5
2519×2492	151	60	57	160	428	27.3	159	73	80	150	462	33.1	−5.8
2520×4649	172	85	82	184	523	31.9	49	33	19	50	151	34.4	−2.5
Total or mean					3,064	31.41					2,686	32.36	−1.41±1.0
(4) Dh 416L3L1C1L1L3L23:													
2541×2524	106	53	38	92	289	31.5	28	6	3	22	59	15.3	16.2
2542×2527	164	55	61	150	430	27.0	133	47	51	129	360	27.2	−.2

2546×2531	95	57	51	99	302	35.8	68	30	26	54	178	31.5	4.3
2549×2537	209	58	67	188	522	23.9	26	3	7	29	65	15.4	8.5
2551×2521	159	88	91	149	487	36.8	37	10	25	44	116	30.2	6.6
2553×2526	146	71	78	150	445	33.5	136	71	78	125	410	36.3	−2.8
2554×2534	169	65	77	147	458	31.0	66	42	24	67	199	33.2	−2.2
Total or mean					2,933	31.0					1,387	30.5	2.66±1.52
(5) Dh 416L3L1C3L21:													
2803×2721	205	39	35	186	465	15.9	461	185	118	631	1,395	21.7	−5.8
2802×2793	206	91	108	238	643	30.9	182	86	52	316	636	21.7	9.2
2812×2783	186	84	67	184	521	29.0	298	89	85	299	771	22.6	6.4
2814×2789	105	46	38	108	297	28.3	81	61	54	102	298	38.6	−10.3
2807×2782	52	138	142	73	405	[1] 30.9	101	409	370	120	1,000	22.1	8.8
Total or mean					2,331	27.16					4,100	23.20	2.19±2.25
(6) Dh 416L3L1C3L1L22:													
2505×2491	226	75	92	250	643	26.0	100	46	30	118	294	25.9	.1
2506×2489	156	58	66	165	445	27.9	212	71	51	267	601	20.3	7.6
2508×2487	387	115	124	368	994	24.0	130	46	50	151	377	25.5	−1.5
2512×2494	196	101	95	202	594	33.0	181	33	37	223	474	14.8	18.2
2513×2492	201	101	104	214	620	33.1	192	80	57	191	520	26.3	6.8
Total or mean					3,296	28.25					2,266	22.11	6.78±2.16
(7) Dh 416L3L1C5L21:													
2884×2870	381	217	238	368	1,204	37.8	486	239	244	425	1,394	34.6	3.2
2887×2873	215	122	120	213	670	36.1	658	309	328	544	1,839	34.6	1.5
2885×2872	117	398	482	112	1,109	[1] 20.6	77	639	651	94	1,461	11.7	8.9
2888×2875	144	99	81	142	466	38.6	394	211	190	369	1,164	34.5	4.1
2893×2869	197	106	113	203	619	35.4	495	226	262	511	1,494	32.7	2.7
Total or mean					4,068	32.57					7,352	29.65	4.97±0.91
(8) Dh 416L3L1C5L4L23:													
2686×2662	169	119	111	169	568	40.3	234	131	146	193	704	39.3	1.0
2682×2663	58	41	47	53	199	44.2	156	61	61	98	376	32.4	11.8
2681×2667	145	87	94	146	472	38.3	81	29	39	61	210	32.4	5.9
3281×2671	203	147	103	264	717	34.9	250	138	147	254	789	36.1	−1.2
2689×2661	252	145	144	221	762	37.9	229	117	110	214	670	33.9	4.0
3488×3684	61	42	46	67	216	40.7	120	62	69	110	361	36.3	4.4
3484×3783	197	123	138	131	589	44.3	163	89	111	188	551	36.3	8.0
Total or mean					3,523	39.4					3,661	35.8	3.76±0.99
(9) Dh416L3L1C5L4L1L24:													
3988×3581	199	92	89	176	556	33.7	310	134	139	241	824	33.3	.4
3984×3592	237	125	131	221	714	35.9	192	94	131	160	577	38.8	−2.9
3993×3600	179	92	103	147	521	37.5	167	92	91	146	496	37.0	.5

[1] Reverse linkage.

TABLE 24.—*Comparison of the rate of crossing over in male and female gametes of plant reciprocals, with summary of seed classes for the individual ears*—Continued

Entry No., progeny designation, and reciprocals	Female parent heterozygous						Male parent heterozygous						Difference (female—male)
	Number of seeds					Per centage of cross-overs	Number of seeds					Per centage of cross-overs	
	Phenotypic classes				Total		Phenotypic classes				Total		
	C Wx	*C wx*	*c Wx*	*c wx*			*C Wx*	*C wx*	*c Wx*	*c wx*			
(9) Dh416L3L1C5L4L1L24—Contd.													
3997×3601	85	51	53	82	271	38.4	167	91	109	151	518	38.5	−.1
3989×3604	160	103	68	157	488	34.5	109	60	56	70	295	39.9	−5.4
3990×3607	84	54	48	77	263	38.8	127	67	81	119	394	37.1	1.7
4009×3614	129	62	69	137	397	32.7	50	34	40	36	160	46.5	−13.8
4000×3615	80	36	30	57	203	33.0	38	27	24	46	135	37.8	−4.8
3996×3616	151	83	79	148	461	35.1	42	22	26	32	122	39.5	−4.4
4010×3618	150	74	62	124	410	33.1	101	74	81	99	355	43.7	−10.6
3978×3640	53	15	19	34	121	28.3	61	34	30	38	163	39.9	−11.6
3986×3642	401	233	239	384	1,257	37.5	210	119	128	197	654	37.7	−.2
4013×3650	89	56	34	69	248	35.8	102	45	50	86	283	33.5	2.3
3982×3653	123	94	75	108	400	42.2	72	63	48	103	286	38.9	3.3
4019×3655	77	39	31	71	218	31.7	143	61	82	122	408	34.9	−3.2
4022×3664	152	91	90	169	502	36.1	183	79	101	128	491	36.8	−.7
4022×3666-2	118	53	38	97	306	29.5	41	29	25	44	139	38.8	−9.3
Total or mean					7,336	35.5					6,300	37.6	−2.85±0.77
(10) Dh 416L3L1C5L3L1R23:													
5901×5700	246	81	87	225	639	26.3	254	59	53	229	595	18.8	7.5
5902×5751	153	38	34	142	367	19.6	273	58	61	214	606	19.6	0.0
5902-2×5701	215	52	49	217	533	18.9	345	67	69	307	788	17.3	1.6
5905×5702	250	112	92	233	687	29.7	152	48	51	128	379	26.1	3.6
5907×5707	235	67	49	269	620	18.7	267	33	47	224	571	14.0	4.7
5909×5710	198	45	38	199	480	17.3	231	53	29	197	510	16.1	1.2
5910×5723	192	108	78	210	588	31.6	229	57	77	195	558	24.0	7.6
5912×5759	65	27	21	69	182	26.4	493	104	128	456	1,181	19.6	6.8
5920×5719	31	3	6	35	75	12.0	196	19	23	233	471	8.9	3.1
5924×5737	297	59	68	284	708	17.9	250	42	48	206	546	16.5	1.4
5925×5720	197	62	49	177	485	22.9	122	40	39	141	342	23.1	−.2
5926×5726	290	59	65	276	690	18.0	271	54	57	214	596	18.6	−.6
5929×5799B	296	89	76	327	788	20.9	189	12	16	141	358	7.8	13.1
5931×5725	47	17	14	37	115	27.0	478	135	151	489	1,253	22.8	4.2
5935×5735	158	21	20	154	353	11.6	243	43	44	189	519	16.8	−5.2

5936×5790	211	41	47	223	522	16.9	310	56	80	282	728	18.7	−1.8
5938×5739	284	43	43	264	634	13.6	92	19	23	90	224	18.7	−5.1
5941–2×5789	158	43	41	167	409	21.0	443	85	103	436	1,067	17.6	3.4
5942×5779	198	68	63	197	526	24.9	228	55	56	250	589	18.8	6.1
5944×5738	170	71	67	172	480	28.7	253	72	70	202	597	23.8	4.9
5946×5741	135	26	26	130	317	16.4	116	16	31	140	303	15.5	.9
5951×5712	229	42	52	214	537	17.5	284	43	49	271	647	14.2	3.3
5961×5726	7	4	4	22	37	21.6	233	78	70	255	636	23.3	−1.7
5970×5764	199	97	106	195	597	34.0	131	56	49	147	383	27.4	6.6
5975×5773	263	57	84	254	658	21.4	264	51	60	230	605	18.3	3.1
5981×5769	164	60	51	188	463	24.0	299	80	60	251	690	20.3	3.7
5982×5780	40	10	13	48	111	20.7	131	25	26	146	328	15.5	5.2
5983×5784	170	23	32	152	377	14.6	160	18	47	110	335	19.4	−4.8
5987×5799G	243	43	48	189	523	17.4	334	45	48	300	727	12.8	4.6
5988×5799F	150	63	79	161	453	31.3	110	34	29	115	288	21.9	9.4
5989×5799D	255	54	54	268	631	17.1	112	27	30	118	287	19.9	−2.8
5990×5792	227	80	65	220	592	24.5	252	53	58	231	594	18.7	5.8
5992×5786	298	60	43	297	698	14.8	56	12	3	76	147	10.2	4.6
6000×5744	218	60	87	214	579	25.4	232	58	66	239	595	20.8	4.6
5918×5716	92	8	51	131	282	8.7	71	23	52	118	264	22.3	−13.6
5927×5736	150	52	100	178	480	26.0	189	25	89	228	531	12.0	14.0
5930×5796	144	38	94	188	464	21.3	165	23	83	196	467	14.0	8.3
5934×5763	319	81	146	421	967	16.6	113	22	71	139	345	18.0	−1.4
5940–2×5778	142	37	90	216	485	19.0	143	27	111	161	442	21.1	−2.1
5943×5777	183	42	79	255	559	14.5	248	52	156	276	732	20.1	−5.6
5950–a×5743	132	32	94	186	444	20.4	370	94	240	563	1,267	19.0	1.4
5958×5709	194	45	120	248	607	19.5	221	42	150	294	707	17.6	1.9
5963×5716	228	54	146	366	794	17.3	126	30	104	196	456	20.7	−3.4
5966×5785	82	23	59	137	301	20.2	154	26	107	159	446	19.6	.6
5979×5767	171	46	121	236	574	21.9	191	27	110	242	570	13.7	8.2
5986×5791	196	41	124	291	652	16.7	239	46	147	300	732	17.3	−.6
5991×5795	207	56	131	299	693	20.1	210	41	139	365	755	15.2	4.8
5994×5799–a	94	16	67	185	362	13.4	139	16	78	200	433	10.7	2.7
5998×5742	163	40	89	217	509	18.0	126	6	56	139	327	5.7	12.3
Total or mean					24,627	20.47					27,517	18.07	2.78±0.49
(11) Dh 416L3L1C5L3L2R23:													
6102×6014	256	59	58	262	635	18.4	206	58	59	161	484	24.2	−5.8
6104×6017	241	99	94	208	642	30.1	146	78	77	133	434	35.7	−5.6
6112×6005	19	7	6	11	43	30.2	142	56	51	170	419	25.5	4.7
6152×6012	231	56	55	222	564	19.7	180	49	71	146	446	26.9	−7.2
6124×6020	145	14	73	187	419	9.6	21	5	13	25	64	20.8	−11.2
6130×6011	127	41	90	172	430	24.2	129	34	105	160	428	24.5	−.3
6138×6028	168	79	130	230	607	30.0	52	23	51	71	197	32.6	−2.6
6160×6019	186	56	139	254	635	23.9	17	3	20	14	54	29.4	−5.5
6106×6027	187	121	16	62	386	19.9	285	179	37	94	595	25.5	−5.6
6120×6010	23	97	149	68	337	19.0	39	58	117	55	269	32.3	−13.3
6131×6016	55	244	224	63	586	20.1	44	102	117	30	293	25.3	−5.2
Total or mean					5,284	22.16					3,683	27.42	−5.60±0.70

TABLE 24.—*Comparison of the rate of crossing over in male and female gametes of plant reciprocals, with summary of seed classes for the individual ears*—Continued

Entry No., progeny designation, and reciprocals	Female parent heterozygous						Male parent heterozygous						Difference (female—male)
	Number of seeds					Percentage of crossovers	Number of seeds					Percentage of crossovers	
	Phenotypic classes				Total		Phenotypic classes				Total		
	C Wx	*C wx*	*c Wx*	*c wx*			*C Wx*	*C wx*	*c Wx*	*c wx*			
(12) Dh 417L1L2L1L21:													
2978×2944	144	43	53	147	387	24.8	194	31	32	199	456	13.8	11.0
2970×2952	156	65	55	164	440	27.3	193	44	47	202	486	18.7	8.6
2975×2947	186	40	33	175	434	16.8	27	1	3	22	53	7.5	9.3
2976×2945	192	51	35	210	488	17.6	201	30	33	197	461	13.7	3.9
2963×2959	118	32	34	125	309	21.4	123	22	31	144	320	16.6	4.8
2966×2954	290	46	47	265	648	14.4	73	11	17	75	176	15.9	−1.5
2980×2943	72	41	27	74	214	31.8	99	20	23	132	274	15.7	16.1
2962×2957	122	41	35	116	314	24.2	137	25	46	143	351	20.2	2.0
2967×2942	117	30	29	98	274	21.5	187	50	49	239	525	18.9	2.6
2971×2960	193	66	57	183	499	24.6	188	30	64	179	461	20.4	4.2
2972×2953	225	46	37	227	535	15.5	188	30	26	191	435	12.9	2.6
2973×2951	66	8	18	42	134	19.4	100	14	28	105	247	17.0	2.4
2965×2956	124	24	37	134	319	19.1	185	33	44	186	448	17.2	1.9
Total or mean					4,995	20.62					4,693	16.71	4.93±0.75
(13) Dh 417L1L2L1L2L23:													
8831×8907	148	37	44	165	394	20.6	45	12	13	27	97	25.8	−5.2
8835×8904	190	71	65	158	484	28.1	189	62	60	162	473	25.8	2.3
8847×8910	120	29	46	123	318	23.6	28	9	4	22	63	20.6	3.0
8853×8903	97	54	40	103	294	32.0	136	74	52	111	373	33.8	−1.8
8857×8922	132	31	29	131	323	18.6	133	38	39	132	342	22.5	−3.9
8815×8910	54	14	15	49	132	22.0	136	50	45	117	348	27.3	−5.3
8820×8913	132	45	42	152	371	23.5	99	36	30	104	269	24.5	−1.0
8824×8903	53	34	23	72	182	31.3	107	64	72	126	369	36.9	−5.6
8843×8917	83	33	46	87	249	31.7	63	24	39	50	176	35.8	−4.1
8848×8913	100	28	36	114	278	23.0	135	61	51	162	409	27.4	−4.4
8855×8909	76	30	25	125	256	21.5	170	87	68	142	467	33.2	−11.7
8858×8922	110	46	55	138	349	28.9	22	9	13	29	73	30.1	−1.2
8859×8919	179	46	68	199	492	23.2	111	39	43	105	298	27.5	−4.3
Total or mean					4,122	25.1					3,757	29.3	−3.48±1.02

Experiments prior to those of Emerson and Hutchison have little bearing on the question, since they were made before the wide fluctuation in the crossing over of individuals was appreciated, and the comparisons were not confined to plant reciprocals.

The pairs of characters studied by Emerson and Hutchison were the *b* and *lg* factors, for plant color and liguleless leaves, and the *c* and *sh* factors, for aleurone color and shrunken endosperm.

The data presented on the *b* and *lg* factors involved 19 reciprocal back crosses and showed no significant difference in the mean crossing over. The behavior of the individual ears is very uniform. The extreme departure from equality in the two sexes is four times the probable error, and in a sample of 20 ears the odds against a departure of this magnitude are only 6 to 1.

Crossing over between *c* and *sh* was measured in two seasons. In 1920, 29 reciprocal back crosses of Emerson and Hutchison (*6*, *Table 3*) gave a mean crossover difference of 1.12 ± 0.186, the lower rate being in the male. The difference is more than six times the probable error. The mean difference is taken from the totals and the probable error is calculated from $\sigma=\sqrt{pq/n}$, wherein n=the total number of seeds. The mean of the array of differences weighted with the reciprocals of their probable errors is 1.30 ± 0.27. Calculated in this way the D/E is slightly lower, but the difference is undoubtedly significant.

Taken by themselves the results of Emerson and Hutchison indicate a significantly lower crossover difference for the character *c–sh* when both recessives enter in the same parent, but since differences of the same order are found between closely related progenies in our material there is little reason for associating the difference with coupling and repulsion series.

TABLE 25.—*Summary comparing the percentages of crossing over in male and female gametes of plant reciprocals*

Entry No. and progeny designation	Number of reciprocals	Female gametes		Male gametes		Difference [1]		
		Number of seeds	Percentage of crossovers	Number of seeds	Percentage of crossovers	♀−♂	Standard deviations	D/E
(1) Dh 416L3L1C1L1L22	4	1,919	24.75	1,885	20.53	3.34±0.50	1.47	6.68
(2) Dh 416L3L1C1L1L1L23	7	3,400	25.80	2,104	24.50	3.42±1.66	6.52	2.06
(3) Dh 416L3L1C1L1L2L23	8	3,064	31.41	2,686	32.36	−1.41±1.00	4.19	1.41
(4) Dh 416L3L1C1L1L3L23	7	2,933	31.00	1,387	30.50	2.66±1.52	5.97	1.75
(5) Dh 416L3L1C3L21	5	2,331	27.16	4,100	23.20	2.19±2.25	7.44	.97
(6) Dh 416L3L1C3L1L22	5	3,296	28.25	2,266	22.11	6.78±2.16	7.18	3.14
(7) Dh 416L3L1C5L21	5	4,068	32.57	7,352	29.65	4.97± .91	3.01	5.46
(8) Dh 416L3L1C5L4L23	7	3,523	39.40	3,661	35.80	3.76± .99	3.87	3.80
(9) Dh 416L3L1C5L4L1L24	17	7,336	35.50	6,300	37.60	−2.85± .77	4.73	3.71
(10) Dh 416L3L1C5L3L1R23	49	24,627	20.47	27,517	18.07	2.78± .49	5.07	5.67
(11) Dh 416L3L1C5L3L2R23	11	5,284	22.16	3,683	27.42	−5.60± .70	3.43	8.00
(12) Dh 417L1L2L1L21	13	4,995	20.62	4,693	16.71	4.93± .75	4.00	6.57
(13) Dh 417L1L2L1L2L23	13	4,122	25.10	3,757	29.30	−3.48±1.02	5.47	3.41
Total	151	70,898		71,391				

[1] The minus sign indicates those cases where there was more crossing over in the male than in the female gametes.

It should be noted in this connection that in the same two series there is a difference in reciprocals with respect to the percentage of white. In the repulsion series in the work of Emerson and Hutchison (*6*, *Table 3*) there is a significantly lower percentage of white when the male is the heterozygous parent (3.2±0.56 per cent), and in the coupling series (*6*, *Table 4*) there is a lower percentage of white when the female is the heterozygous parent (4.0±1.2). These differences statistically are of greater significance than the differences in crossing over.

In view of wide and significant fluctuations in the rate of crossing over that can not be ascribed either to genetic or to know environmental causes, it seems probable that the much smaller differences between the sexes are of the same nature. Until the causes of the variations in crossing over are better understood it will be unsafe to associate differences in the crossing over of reciprocals with differences in sporogenesis.

DIFFERENCES IN CROSSING OVER IN RECIPROCALS WHEN LINKAGE IS NOT OPERATIVE

In making comparisons between the rate of crossing over in male and female gametes where linkage was involved, it was thought desirable to assemble the same sort of data for cases where no linkage was possible.

Table 26 shows the results of reciprocal crosses between white-horny plants heterozygous for waxy (*c c Wx wx*) and colored-waxy plants heterozygous for color (*C c wx wx*). The totals show there is a slight but insignificant difference between the reciprocals in the proportion of the crossover to noncrossover classes.

TABLE 26.—*Reciprocal crosses of colored waxy* (*C c wx wx*) × *white horny* (*c c Wx wx*)

Cross designation	White-horny ♀		Colored-waxy ♀		Difference (colored waxy—white-horny)
	Number of seeds	Percentage of crossovers	Number of seeds	Percentage of crossovers	
3882×3776	290	53.9±1.98	189	50.9±2.45	−3.0±3.15
3885×3787	180	52.3±2.50	198	49.3±2.39	−3.0±3.46
3888×3778	515	47.5±1.48	538	46.9±1.45	−.6±2.07
3892×3784	150	52.5±2.74	72	40.8±3.90	−11.7±4.76
3895×3787–2	61	33.4±4.07	389	50.5±1.39	+17.1±4.24
3898×3793	97	49.6±3.42	26	44.9±6.56	−4.7±7.40
3900×3789	414	47.8±1.65	510	47.5±1.49	−.3±2.28
3907×3802	592	54.7±1.38	445	52.5±1.59	−2.2±2.10
3907–2×3801	224	49.6±2.24	450	51.1±1.59	+1.5±2.75
3909×3804	447	53.4±1.59	628	51.2±1.34	−2.2±2.08
3916×3808	505	50.9±1.50	416	48.1±1.65	−2.8±2.23
3916–2×3808–2	585	49.9±1.39	360	47.7±1.77	−2.2±2.25
3919×3806	438	51.5±1.60	550	49.0±1.43	−2.5±2.14
3922×3803	419	52.3±1.64	256	49.7±2.10	−2.6±2.66
Mean					−1.50± .65

This result was anticipated, but the array of differences is somewhat disturbing. Inspection will show that in 12 of the 14 pairs of reciprocals the proportion of colored-waxy and white-horny seeds was higher when the female parent was white horny. Of the two exceptions, one may be a chance fluctuation, but the other robs the array of its statistical significance. This plus difference results

from a low percentage of the crossover class on a single ear having but 61 seeds. Although the probable error is large, the percentage departs from the mean of the ears of this group by 4.3 times the error, which is rather large to be attributed to errors of random sampling, and there would seem to be some justification for discarding this pair of ears from the data under consideration.

The criterion for the rejection of outlying observations proposed by Irwin (*10*) gives a value for P of less than 0.001. This means that the odds against these observations being a chance departure are more than 1,000 to 1.

If this pair of ears is rejected the mean difference becomes -1.696 ± 0.38, a difference almost 4.5 times the probable error. The magnitude of the difference, as well as its significance, approaches and is comparable with those observed where linkages are present. Such results are disconcerting and tend to discredit the significance of differences observed in the actual rate of crossing over in the two sexes, at least in so far as these differences are attributed to linkage relations.

RATE OF CROSSING OVER NOT ALIKE IN THE UPPER AND LOWER EARS OF THE SAME PLANT

Having found differences in the apparent rate of crossing over between the male and the female, it seemed desirable to carry the analysis a stage further and examine the data for possible differences between upper and lower ears. If the observed differences between male and female were due to differences in environment at the time of the maturation divisions, it seemed not unreasonable that the time elapsing between the divisions in the first and second ears would provide the possibility of a changed environment. To a certain extent upper and lower ears correspond to the broods in Drosophila, where Bridges (*3*) has shown that the rate of crossing over in the second chromosome is lower in the second broods than in the first.

TABLE 27.—*Crossing over in upper and lower ears of progeny Dh 416L3L1C5L3-L1R23 where male gametes are measured and both ears pollinated at the same time*

Parent plant designation ♀ ♂	Upper ear		Lower ear		Difference (lower−upper)
	Number of seeds	Percentage of crossover	Number of seeds	Percentage of crossover	
5702×5905	379	26.1±1.5	82	28.0±3.3	1.9 ±3.7
5710×5909	170	12.9±1.7	340	17.6±1.4	4.7 ±2.2
5725×5931	660	22.3±1.1	593	23.4±1.2	1.1 ±1.6
5759×5912	598	17.9±1.1	583	21.4±1.1	3.5 ±1.6
5718×5903	516	16.3±1.1	566	16.0±1.0	−.3 ±1.5
5743×5950a	564	15.3±1.0	703	22.0±1.0	6.7 ±1.5
5781×5972	525	18.5±1.1	568	21.4±1.2	2.9 ±1.6
5795×5991	266	12.0±1.3	489	16.8±1.1	4.8 ±1.8
Total or mean	3,678		3,924		3.23± .55

If the male gametes are subject to a selective force, it is within the realm of possibilities that the environment afforded by second ears would differ sufficiently from that of the upper ears to bring about differences in the survival of the gametic classes.

The data, therefore, have been examined from the standpoint of upper and lower ears.

Stadler (*16*) measured the rate of crossing over between *C* and *Wx* on the upper and lower ears of 33 plants. Of these pairs, 20 gave a higher rate in the upper ear, but the mean difference was less than 1 per cent and was not statistically significant.

From the white-waxy seeds of Dh 416L3L1C5L3L1R23 there were eight plants each of which had two ears pollinated simultaneously with pollen from the same double-heterozygous plant. The data are presented in Table 27.

The results show a significantly higher crossing over in the second or lower ear. The mean difference is 3.23 ± 0.55 per cent, a difference of 5.8 times the probable error. The individual differences range from -0.3 to 6.7 per cent, but none depart significantly from the mean.

The most obvious difference between upper and lower ears, when both are pollinated on the same day, is the difference in the length of silk at the time of pollination. That this is an important factor is indicated by the ears from two other plants in the same progeny. These plants also produced two ears, each pollinated by the same double-heterozygous plant, but in these cases the lower ear was pollinated two days later than the upper ear. No record was made of the length of silk, but in normal plants of this type the difference in length of silk between upper and lower ears would be more than compensated by the growth in two days. (Table 28.)

TABLE 28.—*Crossing over in upper and lower ears where the lower ears were pollinated two days later than the upper ears*

Parent plant designation	Upper ear		Lower ear		Difference (upper—lower)
	Number of seeds	Percentage of cross-overs	Number of seeds	Percentage of cross-overs	
5787×5999	537	14.1±1.0	212	13.2±1.6	0.9±1.9
5789×5941	256	19.9±1.7	811	16.9± .9	3.0±1.9
Total	793		1,023		2.0± .50

In both of these plants the usual order was reversed and there was a higher crossing over in the upper ear. The mean weighted difference of 2 per cent is four times the probable error, and the mean of these two ears departs from the mean of the eight ears pollinated simultaneously by more than seven times the probable error of the difference.

If delayed pollination of silks is reducing the crossover class in the male gametes, a corresponding difference might be expected between the tip and the base of the ear. No such difference was found in back-crossed ears with the male heterozygous. A mean difference as large as 2 per cent should have been detected in the material studied, but the ears are short and perhaps the silks from the tip and base of the ear do not differ in age sufficiently to effect a differential of this magnitude. Although progeny Dh 416L3L1C-5L3L1R23 would seem to furnish excellent evidence that lower ears

provided conditions more favorable to the development of the crossover classes than upper ears, this condition is not found to be general for all progenies.

A closely related progeny grown at Lanham, Md., in 1924, gave the results shown in Table 29. Ten pairs of ears are listed, which provide a test of the influence of ear position on the proportion of crossover to noncrossover classes in the male gametes. Of these 10 pairs 7 have a higher apparent rate of crossing over in the upper than in the lower ears, and the mean weighted difference in favor of a higher rate for the upper ears is 1.55 ± 0.37 per cent. This difference is more than four times the probable error and is doubtless significant.

From this same progeny there are 17 pairs of ears borne on the heterozygous female plants. These ears provide the opportunity to measure not a selective action on the male gametes but differences in the rate of crossing over in the formation of the gametes of the two inflorescences, or possibly survival rates after the gametes are formed. Of the 17 pairs, 10 show a higher rate of crossing over for the upper ears, but the mean weighted difference of 2.15 ± 0.78 per cent can not be considered significant. The data are also given in Table 29.

TABLE 29.—*Crossing over in upper and lower ears where male and female gametes are measured*

[Progeny Dh 416L3L1C5L4L1-1-L24 for male gametes; progeny Dh 416L3L1C5L4L1-4-L24 for female gametes]

Plant designation	Upper ears		Lower ears		Difference (lower—upper)
	Number of seeds	Percentage of crossovers	Number of seeds	Percentage of crossovers	
Male gametes measured:					
3581×3998	824	33.3±1.11	148	34.0±2.63	0.7±2.86
3601×3997	518	38.5±1.44	181	36.5±2.42	−2.0±2.82
3604×3989	295	39.9±1.92	69	39.2±3.97	−.7±4.42
3618×4010	355	43.7±1.77	371	40.6±1.72	−3.1±2.47
3620×3998	364	37.8±1.71	628	35.6±1.29	−2.2±2.14
3631×3998	596	39.5±1.35	592	37.7±1.34	−1.8±1.91
3442×3986	325	37.7±1.28	86	35.6±2.34	−2.1±2.67
3655×4019	408	34.9±1.59	77	33.0±3.62	−1.9±3.96
3664×4022	491	36.8±1.47	344	39.8±1.78	3.0±2.31
3666×4022	635	37.2±1.29	139	38.8±2.78	1.6±3.06
Mean					−1.55±3.37
Female gametes measured:					
3984	560	35.5±1.36	154	36.4±2.61	.9 ±2.94
3985	698	37.2±1.23	448	31.5±1.47	−5.7 ±1.92
3986	813	38.1±1.15	444	36.4±1.54	−1.7 ±1.92
3988	495	33.3±1.42	61	25.5±3.76	−7.8 ±4.02
3992	166	35.5±2.50	86	35.7±3.48	.2 ±4.28
3993	245	38.8±2.10	276	36.4±1.95	−2.4 ±2.87
3994	355	34.8±1.70	444	37.6±1.55	2.8 ±2.30
3996	434	35.5±1.55	27	29.7±5.92	−5.8 ±6.12
3998	349	33.0±1.70	423	39.0±1.60	6.0 ±2.34
3999	242	39.2±2.12	554	37.9±1.39	−1.3 ±2.53
4000	188	33.6±2.32	15	22.3±7.24	−11.3 ±7.60
4004	118	40.9±3.06	249	34.2±2.03	−6.7 ±3.67
4008	555	40.7±1.40	454	31.0±1.46	−9.7 ±2.02
4009	397	32.7±1.59	355	36.3±1.72	3.6 ±2.34
4010	136	35.8±2.77	410	33.1±1.56	−2.7 ±3.18
4020	410	31.2±1.54	119	34.5±2.94	3.3 ±3.33
4022	502	36.1±1.44	306	29.5±2.95	−6.6 ±2.27
Mean					−2.15± .78

A third progeny bearing on the subject and grown at Arlington, Va., in 1924 is available. This progeny is related to the preceding two in having as one parent a line of Dh 416, but the other parent was an entirely unrelated sweet corn. Data from the pairs of ears testing a possible selective effect of upper and lower ears on the male gametes are shown in Table 30. There are 10 pairs with a mean weighted difference in the direction of a higher percentage of crossovers when the pollen is applied to lower ears of 2.57±1.17. This difference is in the direction of that found in progeny Dh 416L3L1C5L3L1R23, but though in the same direction it can not be considered significant.

TABLE 30.—*Crossing over in upper and lower ears where male and female gametes of progeny Ph 230L1 and L2R24 are measured*

Plant designation	Upper ears		Lower ears		Difference (upper−lower)
	Number of seeds	Percentage of crossovers	Number of seeds	Percentage of crossovers	
Male gametes measured:					
3×110	462	18.7±1.22	319	24.3±1.62	−5.6±2.03
5×200	128	43.9±2.96	317	38.1±1.84	5.8±2.48
6×103	708	23.0±1.07	190	29.5±2.23	−6.5±2.47
15×126	193	29.6±2.21	36	27.4±5.00	2.2±5.46
23×169	265	25.5±1.81	274	35.6±1.95	−10.1±2.66
28×182	465	25.5±1.36	511	24.3±1.28	1.2±1.87
510×616	547	26.7±1.27	282	34.3±1.90	−7.6±2.29
540×720	298	19.2±1.54	324	21.6±1.50	−2.4±2.22
548×603	394	27.6±1.52	407	20.2±1.34	7.4±2.02
16×157	450	24.0±1.36	554	30.1±1.31	−6.1±1.89
Mean					−2.57±1.17
Female gametes measured:					
602×514	508	17.6±1.14	265	18.5±1.60	−.9±1.96
603×548	66	24.6±3.58	51	20.9±3.82	3.7±5.23
616×510	118	18.1±2.90	320	15.7±1.36	2.4±2.77
624×506	69	37.8±3.92	79	29.2±3.44	8.6±5.22
644×522	234	21.2±1.80	76	17.2±2.92	4.0±3.42
674×807	332	24.5±1.59	42	30.5±4.80	−6.0±5.05
677×519	451	11.6±1.01	125	31.2±2.80	−19.6±2.97
684×533	60	25.4±3.80	180	19.0±1.97	6.4±4.29
103×1	649	14.9± .94	450	15.2±1.18	−.3±1.48
117×1	260	21.5±1.72	756	25.7±1.05	−4.2±2.02
119×10	524	17.7±1.16	140	14.9±2.02	2.8±2.32
120×6	344	26.5±1.60	359	21.0±1.45	5.5±2.16
126×8	681	23.6±1.10	135	19.2±2.28	4.4±2.53
139×35	379	7.6± .92	128	12.5±1.97	−4.9±2.18
144×29	549	25.2±1.25	335	13.5±1.26	11.7±1.77
147×25	396	15.3±1.22	67	18.0±3.16	−2.7±3.39
149×13	520	8.8± .84	277	10.0±1.22	−1.2±1.48
157×16	398	18.5±1.31	330	19.3±1.46	−.8±1.97
158×7	197	13.6±1.65	523	18.6±1.18	−5.0±2.00
163×28	538	18.6±1.16	467	16.6±1.16	2.0±1.62
164×13	447	19.5±1.26	411	25.7±1.45	−6.2±1.92
169×23	596	20.5±1.11	548	19.7±1.18	.8±1.59
178×26	383	14.2±1.20	443	11.5±1.02	2.7±1.57
179×26	321	28.1±1.66	223	33.6±2.60	−5.5±2.70
184×33	455	23.6±1.34	148	19.5±2.20	4.1±2.57
187×33	165	7.6±1.39	271	15.5±1.47	−7.9±2.03
191×34	321	16.7±1.40	124	12.2±1.97	4.5±2.42
203×14	669	16.7± .97	335	15.2±1.32	1.5±1.67
213×3	161	21.5±2.18	286	21.2±1.63	.3±2.71
216×5	611	25.6±1.19	367	24.3±1.50	1.3±1.91
222×1	365	16.7±1.32	318	32.0±1.76	−15.3±2.20
210×3	371	18.4±1.35	99	22.0±2.79	−3.6±2.15
Mean					−.43± .67

From this same progeny 32 pairs of ears are available showing the difference in rate of crossing over between the upper and lower ears when the female parent is heterozygous. Data from these ears

are also shown in Table 30. The differences are extremely variable, ranging from −19 to 11. The mean weighted difference of 0.43± 0.67 per cent is in the direction of more crossing over in the second ears, but obviously this is without significance.

The three progenies examined all showed differences of comparable magnitude between upper and lower ears in the proportion of crossover to noncrossover seeds where the male was the heterozygous parent. Two of these progenies had the highest proportion of crossover seed on the lower ears; the third being the reverse, with a higher proportion of crossover in the upper ears.

Since these differences are found when the male parent is heterozygous, and apparently only then, there can be no question of a different rate of crossing over in the formation of the gametes, and the differences observed could arise only as the result of some sort of selective action operating on the male gametes after they were formed.

Only two progenies afforded material for testing differences in crossing over between upper and lower ears when the female was the heterozygous parent. These progenies were consistent in that no differences were found. It would seem, therefore, that even though environment has an effect on the proportions of gametic classes, the time elapsing between the maturation division in the upper and lower ears does not provide a period sufficiently long to bring about a change in the rate of crossing over. Furthermore, it seems clear that no consistent death rate operates among the female gametes, the lower ears having no higher rate of crossing over than upper ears.

RATE OF CROSSING OVER NOT ALIKE IN BASE AND TIP OF THE SAME EAR

The seeds of an ear of maize develop under closely similar environmental conditions. Nevertheless, owing to the length of the ear, the seeds from the base and tip are subjected during fertilization to slightly different conditions.

Silks from the base of the ear emerge earlier and in consequence are older at the time of pollination than the silks from the tip. In extreme cases the difference in time of appearance may be as much as two or three days. In cases of this sort it is obvious that the pollen tubes fertilizing ovules at the tip of the ear have an advantage over those fertilizing basal ovules, since they have not only a shorter distance to grow but also younger tissue in which to develop.

In view of these advantages, if the apparent crossing over in the male is influenced by differential mortality of the male gametes or a differential growth rate of the pollen tube, one might expect a difference in crossing over between the base and the tip of the ear. If the crossover class were the weaker it might achieve fertilization less frequently in ovules at the base than at the tip of the ear.

From two sister progenies grown at Arlington, Va., in 1923, 79 well-formed ears were selected. The seeds from the base and from the tip of these ears were classified separately. Since the silks from the extreme base of the ear often are delayed in emerging, a few seeds from the base of the ear were excluded from the comparison.

With the idea of disclosing a trend from tip to base in the percentage of crossing over, some of the larger ears were divided into

cross sections of approximately 100 seeds each, and the crossing over in each section was measured separately. The fluctuations in such small samples were too large to detect any consistent differences at different levels, and these ears were included with those classified into tip and base by discarding the basal section and combining the remainder into two groups.

The ears included back crosses between double-heterozygous plants and double recessives and self-pollinated double-heterozygous plants. Ears with both monohybrid and dihybrid ratios of white to colored were included, and since there are significant differences in the crossover ratio of different individuals the mean ratio is of no significance. But the base and the tip of each ear are always of the same composition and are measured in the same way, hence it seems a proper procedure to average the differences between the crossing over of base and tip, the differences being weighted by the reciprocals of their squared probable errors.

The results show a difference between the rate of crossing over at the base and at the tip of the ear, with the higher rate occurring in the tip of the ear. Contrary to expectation, however, the difference is evident only when the female is the heterozygous parent. In the 43 ears of the progeny L1, all of which were from heterozygous females, the percentage of crossing over in the tip exceeded that in the base by 1.29 ± 0.49 per cent. In the progeny L2 the 26 ears with the female heterozygous showed a mean difference in the same direction of 2.79 ± 0.87 per cent. Combining the ears of both progenies having the female heterozygous, the difference is 1.80 ± 0.44, which is 4.1 times its probable error. In the 10 ears of the L2 progeny with the male parent heterozygous there was practically no difference in the crossing over in the base and in the tip of the ear. The mean difference was 0.98 ± 0.40 per cent, the higher crossover ratio being in the seeds from the base of the ear. The individual ears are listed in Table 31. As a check on the reliability of the difference in crossing over, a similar comparison of the tip and the base of the ears was made with respect to the percentages of white and of waxy. The results showed that in the simple Mendelian characters there were no significant differences between the tip and the base of the ears.

TABLE 31.—*Differences in percentages of crossing over in tip and base*

Ear No.	Tip		Base		Difference (tip−base)
	Number of seeds	Percentage of crossovers	Number of seeds	Percentage of crossovers	
Dh 416L3L1C5L3L1R23, female heterozygous:					
5901	334	27.8	305	24.6	3.2 ±2.3
5902-2	210	18.6	323	19.2	−.6 ±2.3
5905	348	34.2	339	25.1	9.1 ±2.3
5907	288	18.4	332	19.0	−.6 ±2.1
5910	278	31.6	310	31.6	0.0 ±2.6
5922	326	18.4	348	14.4	4.0 ±1.9
5923	180	30.6	240	26.7	3.9 ±2.0
5928	294	26.9	323	23.2	3.7 ±2.3
5929	368	18.5	420	23.1	− 4.6 ±1.9
5931	59	27.1	56	26.8	.3 ±5.6
5935	161	13.0	192	10.4	2.6 ±2.3

TABLE 31.—*Differences in percentages of crossing over in tip and base*—Contd.

Ear No.	Tip		Base		Difference (tip−base)
	Number of seeds	Percentage of crossovers	Number of seeds	Percentage of crossovers	
Dh 416L3L1C5L3L1R23, female heterozygous—Continued.					
5946	196	19.4	121	11.6	7.8 ±2.7
5952	304	25.7	328	18.9	6.8 ±2.2
5964	444	17.8	509	22.0	−4.2 ±1.7
5970	309	35.2	288	32.6	2.6 ±2.6
5984	205	20.0	202	16.8	3.2 ±2.6
5985	184	26.6	220	21.8	4.8 ±2.9
5987	188	17.5	335	17.3	.2 ±2.3
5989	277	18.4	354	16.1	2.3 ±2.0
5990	291	25.4	301	23.6	1.8 ±2.4
5909	192	14.0	196	16.8	−2.8 ±2.5
5944	197	33.0	194	23.2	9.8 ±3.1
5978	300	19.3	319	19.4	−.1 ±2.1
5981	166	21.1	197	25.4	−4.3 ±3.0
5918	145	7.0	137	11.0	−4.0 ±2.3
5927	262	28.6	218	22.8	5.8 ±2.7
5930	214	19.5	250	22.9	−3.4 ±2.6
5957	183	25.1	185	30.2	−5.1 ±3.1
5958	307	21.9	300	15.3	6.6 ±2.1
5963	343	16.6	451	18.0	−1.4 ±1.8
5991	353	20.2	340	19.5	.7 ±2.0
5994	161	15.1	201	10.5	4.6 ±2.4
5943	247	14.6	204	14.4	.2 ±2.2
5944-2	323	26.0	308	21.0	5.0 ±2.2
5954	363	22.8	364	20.7	2.1 ±2.0
5981-2	77	17.6	103	16.4	1.2 ±3.8
5908-2	128	25.1	113	34.2	−9.1 ±3.8
5929-2	183	17.9	152	24.1	−6.2 ±3.0
5934-2	144	10.1	109	29.6	−19.5 ±3.4
5955-2	93	19.7	127	13.1	6.6 ±3.4
5959	137	16.2	170	23.5	−7.3 ±3.0
5987-2	223	18.9	263	14.8	4.1 ±2.3
5996-2	94	31.2	125	18.2	13.0 ±4.0
Mean					1.29± .49
Dl 416L3L1C5L3L2R23, female heterozygous:					
6102	316	20.2	209	17.2	3.0 ±2.3
6104	270	29.6	273	30.7	−1.1 ±2.7
6131	286	21.0	204	18.6	2.4 ±2.4
6134	304	21.7	237	19.4	2.3 ±2.3
6142	122	31.1	203	30.0	1.1 ±3.6
6146-2	324	37.0	310	28.4	8.6 ±2.5
6152	186	26.3	255	18.0	8.3 ±2.7
6120	136	23.5	102	15.6	7.9 ±3.5
6124	199	10.4	111	3 3	7.1 ±1.8
6130	198	27.1	125	26.8	.3 ±3.5
6136	362	15.3	299	18.4	−3.1 ±1.9
6138	302	33.8	203	29.0	4.8 ±2.8
6150	177	12.7	211	19.4	−6.7 ±2.5
6157	127	30.4	100	28.9	1.5 ±4.1
6159	146	21.3	101	21.9	−.6 ±3.6
6160	300	29.9	230	20.1	9.8 ±2.5
6106	184	18.7	103	13.5	5.2 ±2.9
6139	180	11.2	229	22.8	−11.6 ±2.4
6126	222	33.9	306	25.1	8.8 ±2.7
6152a	368	17.4	309	19.9	−2.5 ±2.0
6102-2	297	19.5	212	17.9	1.6 ±2.4
6137	156	25.9	106	15.8	10.1 ±3.3
6146	251	29.2	214	20.4	8.8 ±2.7
6164	89	41.9	94	20.6	21.3 ±4.5
6130-2	245	18.9	315	23.4	−4.5 ±2.3
6150-2	125	31.3	120	11.6	19.7 ±3.5
Mean					2.79± .87
Dh 416L3L1C5L3L2R23, male heterozygous:					
6005	205	26.3	106	27.4	−1.1 ±3.6
6012	140	26.4	201	30.3	−3.9 ±3.3
6014	202	24.8	180	22.8	2.0 ±3.0
6024	272	33.1	220	35.5	−2.4 ±2.9
6017	160	34.4	140	36.4	−2.0 ±3.7
6016	170	24.1	123	26.8	−2.7 ±3.5
6025	225	13.4	213	13.8	−.4 ±2.2
6010	120	34.2	149	31.4	2.8 ±3.9
6020	122	40.0	101	39.2	.8 ±4.5
6027	219	24.5	281	26.5	−2.0 ±2.6
Mean					−.98± .40

It appears that in these two progenies there is a small but significant difference in the rate of crossing over at the base and at the tip of the ear. This difference is confined to the formation of female gametes and is not found when the male is the heterozygous parent. It should be kept in mind that the results are based on the behavior of two closely related progenies. These same two progenies, however, showed a striking difference in the relative frequency of crossing over in male and female.

The most obvious difference in the conditions of fertilization of the base and tip of the ear where the plant bearing the ear is heterozygous is the greater promptness with which fertilization is effected at the tip of the ear. This difference suggests a differential mortality of female gametes as the cause of the lower crossing over at the base of the ear. It is difficult, however, to reconcile this explanation with the regular arrangement of the seeds on the ears measured and with the lack of correlation between crossing over and silk length considered later.

LENGTH OF SILK NOT A FACTOR IN RATE OF CROSSING OVER

In seeking an explanation for the greater percentage of crossing over on second ears as compared with first or upper ears of the same plants, the thought naturally occurred that the difference between the two ears might be due to a difference in length of silks.

TABLE 32.—*Differences in crossover rate when measured on ears with long and short silks*

[The differences are between pairs of ears pollinated simultaneously and measure crossing over in female and male gametes respectively]

Designation	Silk length (inches)			Difference in crossovers (per cent) [1]
	Long	Short	Difference	
Female gametes	5	4	1	−4.7 ±3.64
	3	1	2	2.8 ±5.02
	4	¾	3¼	−0.7 ±2.91
	8	¾	7¼	−1.0 ±2.37
	3	1	2	−3.6 ±3.75
	8	4	4	−1.6 ±2.44
	3	1	2	−0.3 ±4.04
	3	1	2	−1.4 ±2.86
	4	½	3½	3.5 ±3.11
	4	2	2	−3.0 ±2.33
	6	4	2	−1.9 ±1.61
	5	1	4	−2.5 ±1.58
	3	1	2	5.3 ±2.72
	4	1½	2½	0.8 ±1.95
	4	1	3	−2.6 ±2.76
	5	3	2	−10.1 ±3.41
Mean	4.5	1.7	2.7	−1.36± .51
Male gametes	3	2	1	4.8 ±2.02
	7	2	5	−7.8 ±2.02
	3	¾	2¼	5.8 ±5.14
	4	2	2	5.0 ±3.86
	3	2	1	5.0 ±2.00
	3	1	2	−1.7 ±5.45
Mean	3.8	1.6	2.2	1.01±1.71

[1] Minus sign indicates those cases where the highest percentage of crossing over occurred with the long silks.

With normal corn plants the silks of the upper ear are the first to appear, and if the two ears are pollinated on the same day the silks of the upper ears would be the longer. Accordingly, an effort was made to test this possibility by recording the length of the silks at the time of pollination and cutting back the silks of the upper ear until these silks were exceeded by those of the second ear.

This program was followed on double-heterozygous and double-recessive plants and the ears back crossed. Paired pollinations were made simultaneously. If the length of the silk was the determining factor, it could come into operation only when the male parent was heterozygous, whereas if the length merely served as an index of age of gamete its influence would be shown when the female parent was heterozygous and the pollen all of one kind, namely, double recessive.

The data for both heterozygous male and heterozygous female plants are given in Table 32. In examining this table it should be borne in mind that the differences shown are between upper and lower ears in each case, both ears having been fertilized by pollen from the same male parent, thus eliminating differences between plants.

The minus sign is used to indicate those cases where the highest crossing over was found on the ears having the longest silks.

The difference in crossover rates is smaller, though not significantly so, when heterozygous pollen is used than when the female parent is heterozygous, but it is apparent that length of silk either as such or as an index of age of gamete is not an appreciable factor in determining the percentage of crossing over.

Eight pairs of ears are available on heterozygous female plants where there was no difference between the ears in silk length, and four such pairs are available where the male parent was heterozygous. Though the number of pairs in each case is small, they afford an opportunity to determine whether the rate of crossing over varies more in those pairs where differences in silk length were involved than in those where no difference in silk length existed. This comparison is made by squaring the differences between the pairs and dividing by the $\sqrt{2}$, since differences between ears and not the departure from their mean are involved.

Where the female gametes are measured and a mean difference in silk length of 2.68 inches exists, the standard deviation is 2.30 ± 0.27 per cent, and where there was no difference in silk length it is 5.18 ± 0.87. A similar situation is found with respect to the male gametes. Thus, where a mean difference in silk length of 2.2 inches existed the standard deviation is 4.45 ± 0.87, and where there was no difference in silk length it is 5.22 ± 1.25 per cent.

From these comparisons it seems clear that silk length is not a factor in bringing about differences in crossover rates.

VARIATIONS IN METEOROLOGICAL CONDITIONS DURING ANTHESIS NOT A FACTOR IN RATE OF CROSSING OVER

Plants of the progeny Dh 416L3L1C5L3L1R23 were flowering during a period of 15 days. During this period the mean daily temperature showed a fluctuation of 10 degrees F., and on August 17 there was a rainfall of 0.91 inch, terminating a protracted drought.

If changes in temperature or humidity at the time of pollination influenced the apparent rate of crossing over there would be detectable differences in the mean rate of crossing over of ears pollinated at different dates. The mean rate of crossing over for all days on which four or more pollinations were made are presented in Table 33. Differences in the rate of crossing over in male and female gametes and in the presence of heterozygous or homozygous *R* make it necessary to subdivide the ears into four groups and to confine comparisons to the ears of the same group.

TABLE 33.—*Crossing over measured on ears of Dh 416L3L1C5L1R23 pollinated on different dates*

Date of pollination	Female heterozygous				Male heterozygous			
	R R		*R r*		*R R*		*R r*	
	Number of ears	Percentage of cross-overs	Number of ears	Percentage of cross-overs	Number of ears	Percentage of cross-overs	Number of ears	Percentage of cross-overs
Aug. 11			4	18.8±1.51			5	17.4±0.99
Aug. 14					6	17.4±0.74	5	18.8± .77
Aug. 16	13	19.9±0.82	6	17.9± .49	14	20.3± .62	10	15.0±1.30
Aug. 20			6	21.3±1.86	24	18.3± .62	19	17.6± .59
Aug. 23	19	22.2± .94			9	18.6± .54	8	18.0±1.14

The most significant difference is that between August 14 and 16 in the *R R* group of male heterozygous. The difference is 2.9±0.97 per cent, which is three times the probable error. This departure is not too large to be ascribed to chance, for the difference is the largest of 20 possible comparisons. The magnitude, however, is of the same order as the variations significantly associated with other factors. The absence of any significant correlation between crossing over and the date of pollination is evidence that there is no progressive change in the rate of crossing over as the season advances, but daily fluctuations would not be reflected in this correlation.

In seeking an explanation for differences between families in the rate of crossing over of *C* and *Wx*, Stadler (*16*) considered differences in flowering dates and concluded that there was no apparent relation of flowering dates to crossover percentages.

Another method of detecting daily fluctuations is to compare the mean standard deviation of crossing over on individual days with the standard deviation of the entire population. If the mean rates of crossing over on individual days differ among themselves more widely than should follow as the result of random sampling, the mean standard deviation on individual days should be less than that for the entire population. The mean standard deviation of crossing over of ears pollinated on the same day is 4.81±0.19, and that for the entire population is 4.57±0.16. The results indicate that the crossing over of ears pollinated on individual days were random samples from the general population and that changes in the meteorological conditions at the time of pollination did not influence the apparent rate of crossing over.

RATE OF CROSSING OVER SIMILAR IN FIRST AND LAST POLLEN SHED

Eight plants are available from a single progeny from which the first pollen shed was used and a further sample taken after a lapse of several days. The data from these plants, shown in Table 34, can be used to test any change associated with the age of the plant.

The mean time difference between the first and last samples of pollen was 4.66 days, and the rate of crossing over was 0.48 ± 0.86 per cent greater for the early samples than for the late ones. This difference can not be considered significant, and with the population of eight plants a difference of 3 per cent could have been detected.

A further test of changes in the rate of crossing over associated with the increase in age of the parent is found in a second progeny where each of seven plants functioned twice as male parents with a lapse of one day or more in time between the two applications of pollen. These cases are also shown in Table 34. In this progeny the greater rate of crossing over is found in the late pollen, though the difference is not significant.

TABLE 34.—*Percentage of crossing over in first pollen shed compared with that shed at a later date*

Heterozygous plant	Early pollen		Late pollen		Difference	
	Number of seeds	Per centage of crossovers	Number of seeds	Per centage of crossovers	Per centage of crossovers [1]	Number of days
Progeny Dh 416L3L1C1L1L2-1-L23:						
No. 2507	350	17.1±1.60	18	11.1±7.05	6.0 ±7.26	9.5
No. 2518	719	37.8±1.22	71	32.4±3.55	5.4 ±3.75	2.0
No. 2520	1,068	36.2± .99	151	34.4±2.42	1.8 ±2.62	3.0
No. 2514	278	27.7±1.81	606	20.6±1.21	7.1 ±2.18	4.5
No. 2509	402	21.6±1.49	903	22.9± .94	−1.3 ±1.77	5.0
No. 2519	462	33.1±1.39	493	30.7±1.40	2.4 ±1.97	5.5
No. 2510	337	19.0±1.63	413	22.8±1.47	−3.8 ±1.68	5.5
No. 2511	1,211	27.0± .85	226	28.7±2.03	−1.7 ±2.20	2.0
Mean					.48 ± .86	4.66
Progeny Dh 416L3L1C5L3L1R23:						
No. 5901	61	11.5±2.76	595	18.8±1.04	−7.3 ±2.94	4
No. 5902	606	19.6±1.09	788	17.3± .91	2.3 ±1.41	6
No. 5903	566	16.0±1.03	516	16.3±1.09	−.3 ±1.51	1
No. 5916	602	16.1±1.00	210	19.7±1.85	−3.6 ±2.10	4
No. 5919	599	29.0±1.18	834	27.6±1.04	1.4 ±1.53	6
No. 5938	224	18.7±1.75	602	23.4±1.16	−4.7 ±2.10	3
No. 5941	256	19.9±1.68	811	16.9± .88	3.0 ±1.90	6
Mean					−.146± .871	4.3

[1] Minus sign indicates those cases where more crossing over occurred in the late pollen. The probable error given has been corrected for the size of the population.

Combining the two progenies, the mean difference becomes 0.128 ± 0.604 per cent, with a greater crossing over in the early pollen. This difference, of course, is not significant, and a consideration of the probable errors shows that a difference of 2 per cent could have been detected.

There would seem to be no reason to believe that the rate of crossing over between *C* and *Wx* changes appreciably with the advance of time, even though the period over which the gametes are forming probably is as long as the period involved in the present comparisons.

From the mean difference between these paired ears it is not possible to determine whether environmental factors operative at

the period of reduction divisions have an effect on crossing over. The plants considered in the present groupings flowered during a period of a week or more, and if unfavorable climatic conditions affected the gametes this effect would be observed on the early gametes of one plant and on the late gametes of another. A combined population would mask such effects, but a consideration of the individual differences shows that none is greater than three times the probable error, and all reasonably may be ascribed to chance.

The probable errors are so large, however, that no final conclusions as to the lack of influence of environmental factors can be drawn. The evidence merely indicates that factors operating during the period of reduction division are not critical with respect to the rate of crossing over.

CORRELATIONS

If apparent crossing over is influenced by the condition of the parent plants, it was thought this might be reflected in a correlation between vigor (as measured by the number of seeds produced) and the rate of crossing over. Very definite evidence of this was found in the data that had accumulated before 1923. Forty reciprocal crosses measuring the linkage between *C* and *Wx* made prior to 1923 showed a positive correlation of 0.51 ± 0.08 between the percentage of crossing over in the male gametes and the number of seeds produced on the ear of the double-recessive-plant fertilized by the heterozygous pollen. There also was a correlation of practically the same magnitude (0.56 ± 0.07) between the rate of crossing over in the female gametes and the number of seeds on the double-recessive plant. With the idea of following up the suggested relationship indicated in these early experiments, an effort was made to amass a larger population derived from a single progeny in one season.

The results of this effort were successful in that 47 reciprocal back-crossed ears were obtained in a single progeny, but the data show the relationship to be much less close than in the earlier experiment. The correlation between the crossing over in the male and number of seeds on the recessive plant was 0.24 ± 0.09. The correlation is a little less than three times the probable error. That this correlation, though small, is significant is indicated by the results from the entire progeny, including ears not reciprocals. The crossing over in the male was measured in 112 individuals, and the correlation between the crossing over and number of seeds produced on the double-recessive plant is 0.28 ± 0.06. This is in close agreement with the coefficient found in the population restricted to reciprocals, but is more than four times the probable error.

A further examination of the data prior to 1923 indicates that the large coefficients were the result of interprogeny correlations. Ten progenies were involved, and when the mean crossing over in the male is plotted against the mean number of seeds on the recessive plants there is a coefficient of 0.78 ± 0.15. The number is so small and the means are derived from populations that vary so greatly in size that no importance should be attached to this coefficient beyond an interpretation of the positive correlation found in the combined population.

TABLE 35.—*Correlation coefficients of the characters in the ears of 47 plant reciprocals from a single progeny*

[Progeny Dh 416L3L1C5L3L1R23. Each coefficient greater than 0.3 (in italic type) exceeds three times its probable error]

Designation of characters	Characters of the ears borne on double-heterozygous plants								Characters of the ears borne on double-recessive plants								Difference in crossovers
	Number of seeds	Percentage of white	Percentage of waxy	Percentage of crossovers in female	Ear length	Base without seeds	Number of rows	Date of pollination	Number of seeds	Percentage of white	Percentage of waxy	Percentage of crossovers in male	Ear length	Base without seeds	Number of rows	Date of pollination	
Characters of the ears borne on double-heterozygous plants:																	
Number of seeds	-------	0.167	0.020	0.110	*0.398*	*−0.400*	0.286	−0.204	−0.118	0.192	.090	0.078	−0.134	0.219	−0.187	−0.179	0.006
Percentage of white	0.167	-------	*.513*	.224	−.118	−.126	.045	−.134	.228	.268	.144	.090	.176	−.045	.244	.134	.126
Percentage of waxy	.020	*.513*	-------	.032	−.063	.063	.190	.134	.017	.014	−.020	.032	−.045	−.045	−.063	−.017	.009
Percentage of crossovers in female	.110	.224	.032	-------	−.179	−.224	.090	−.078	.208	.110	−.032	*.487*	.199	.078	.220	.110	*.578*
Ear length	*.398*	−.118	−.063	−.179	-------	.232	−.126	−.239	.055	.063	.078	−.125	−.055	.130	−.090	−.138	−.095
Base without seeds	−*.400*	−.126	.063	−.224	.232	-------	−.237	−.009	−.134	−.134	−.071	−.255	−.190	−.110	−.274	−.206	.006
Number of rows	.286	.045	.190	.090	−.126	−.237	-------	−.010	−.210	.055	−.100	−.063	−.173	.155	−.090	−.063	.148
Date of pollination	−.204	−.134	.134	−.078	−.239	−.009	−.010	-------	−*.346*	−*.302*	−*.306*	−.010	−.032	.245	.032	*.573*	−.028
Characters of the ears borne on double-recessive plants:																	
Number of seeds	−.118	.228	.017	.208	.055	−.134	−.210	−*.346*	-------	.126	.114	.241	*.571*	−*.388*	*.592*	.210	.001
Percentage of white	.192	.268	.014	.110	.063	−.134	.055	−*.302*	.126	-------	*.731*	−.010	−.100	−.084	−.114	−.206	.100
Percentage of waxy	.090	.144	−.020	−.032	.078	−.071	−.100	−*.306*	.114	*.731*	-------	−.064	−.095	−.185	−.261	−*.300*	−.002
Percentage of crossovers in male.	.078	.090	.032	*.487*	−.125	−.255	−.063	−.010	.241	−.010	−.064	-------	.187	−.200	.206	.239	−*.417*
Ear length	−.134	.176	−.045	.199	−.055	−.190	−.173	−.032	*.571*	−.100	−.095	.187	-------	.161	*.775*	*.581*	.026
Base without seeds	.219	−.045	−.045	.078	.130	−.110	.155	.245	−*.388*	−.084	−.185	−.200	.161	-------	.090	.239	.237
Number of rows	−.187	.244	−.063	.220	−.090	−.274	−.090	.032	*.592*	−.114	−.261	.206	*.775*	.090	-------	*.747*	.054
Date of pollination	−.179	.134	−.017	.110	−.138	−.206	−.063	*.573*	.210	−.206	−*.300*	.239	*.581*	.239	*.747*	-------	−.100
Difference in crossovers	.006	.126	.009	*.578*	−.095	.006	.148	−.028	.001	.100	−.002	−*.417*	.026	.237	.054	−.100	-------

The coefficients of correlation of a series of characters for 47 pairs of reciprocal back-crossed ears are given in Table 35. Most of the characters included are self-explanatory. With the exception of "difference in crossover," the characters are repeated in the reciprocal ears. Difference in crossover is the percentage of crossing over in the female gametes as measured on the double-heterozygous plant minus the percentage of crossing over in the male gametes measured on the ear produced on the double-recessive plant. The character "Base without seeds" is the distance from the base of the cob to the first seed borne on the ear. This character was included as being an indication of imperfect pollination that might be associated with weak pollen or ovules. Coefficients that exceed three times the probable error have been printed in italic type. These are few in number and for the most part are of a physical nature. The correlation of 0.487 ± 0.075 between the crossing over in male and female gametes, when compared with the absence of significant correlations between the percentages of white or waxy in the two sexes, is strong evidence that there is markedly more individual diversity in the rate of crossing over than there is in Mendelian ratios.

In all comparisons involving the crossing over in both sexes, it was necessary to confine the material to reciprocal crosses. Additional material was available, however, for the characters confined to single ears. Table 36 gives the correlation coefficients for characters of back-crossed ears grown from seeds that were double heterozygous and double homozygous, respectively. To the characters included in the table of reciprocals there has been added "Number of seeds per centimeter" and "Mean weight of seeds." The first is the total number of seeds divided by the length of the ear expressed in centimeters.

The only character significantly correlated with crossing over is the number of seeds in the ears, measuring the crossing over in the male, 0.278 ± 0.059. This was mentioned in connection with the explanation of the earlier data. The corresponding correlation in the ears produced on double-heterozygous plants is 0.042 ± 0.073. These coefficients indicate that in this progeny at least a differential death rate is operative on the male but not on the female gametes.

If the vigor of the homozygous plant on which the crossing over in the pollen is measured were affecting the survival of the crossover class, it should have been apparent in the correlations between crossing over in the male and certain characters, namely, ear length, number of rows, and mean weight of seed. These coefficients, though insignificant, are all positive in sign. On the other hand, the absence of any correlation between crossing over in the female and the number of seeds on the ear measuring the crossing over is in accord with the correlations with the other measures of vigor, two of which are negative in sign, that with mean weight of seed being nearly three times the probable error.

TABLE 36.—*Correlation coefficients in all ears where male is heterozygous (progeny Dh 416L3L1C5L3L1–1–R23) and where female is heterozygous (progeny Dh 416L3L1C5L3L1–4–R23)*

[Each coefficient (in italic type), if greater than 0.185 in the upper half of the table or if greater than 0.210 in the lower half of the table, exceeds three times its probable error]

Designation of progeny and characters	Number of seeds	Percentage of white	Percentage of waxy	Percentage of crossovers	Ear length	Base without seeds	Tip without seeds	Number of rows	Date of pollination	Number of seeds per centimeter	Mean weight of seeds
Progeny Dh 416L3L1-C5L3L1-1-R23(male heterozygous):											
Number of seeds		0.005	0.161	*0.278*	*0.527*	*−0.536*	−0.135	*0.551*	−0.171	*0.705*	−0.026
Percentage of white	0.005		*.701*	−.085	.125	.074	−.078	−.078	−.032	−.039	*.194*
Percentage of waxy	.161	*.701*		.042	*.220*	.03	−.103	−.014	−.063	.080	.107
Percentage of crossovers	*.278*	−.085	.042		.162	−.129	−.097	.106	−.091	.175	.002
Ear length	*.527*	.125	*.220*	.162		−.037	.118	*.279*	−.104	.009	*.278*
Base without seeds	*−.536*	.074	.030	−.129	−.037		.057	−.143	−.07	*−.486*	.026
Tip without seeds	−.135	−.078	−.103	−.097	.118	.057		−.109	.051	.109	.033
Number of rows	*.551*	−.078	−.014	.106	*.279*	−.143	−.109		−.126	.124	−.036
Date of pollination	−.171	−.032	−.063	−.091	−.104	−.070	.051	−.126		−.121	*−.220*
Number of seeds per centimeter	*.705*	−.039	.080	.175	.009	*−.486*	.109	.124	−.121		*−.248*
Mean weight of seeds	−.026	*.194*	.107	.002	*.278*	.026	.033	−.036	*−.220*	*−.248*	
Progeny Dh 416L3L1-C5L3L1-4-R23 (female heterozygous):											
Number of seeds		.075	−.017	.042	*.564*	*−.388*	*−.339*	*.478*	*−.212*	*.665*	−.165
Percentage of white	.075		*.463*	.024	−.082	.004	.089	.026	−.063	.156	*−.232*
Percentage of waxy	−.017	*.463*		−.089	−.075	.075	.175	.113	.082	.093	*−.220*
Percentage of crossovers	.042	.024	−.089		−.141	−.166	−.085	.004	.035	.113	−.205
Ear length	*.564*	−.082	−.075	−.141		.135	−.077	.186	−.203	−.104	.191
Base without seeds	*−.388*	.004	.075	−.166	.135		.190	*−.307*	.024	*−.381*	.147
Tip without seeds	*−.339*	.089	.175	−.085	−.077	.190		.004	.173	−.169	.073
Number of rows	*.478*	.026	.113	.004	.186	*−.307*	.004		−.189	.145	−.206
Date of pollination	*−.212*	−.063	.082	.035	−.203	.024	.173	−.189		−.042	−.049
Number of seeds per centimeter	*.665*	.156	.093	.113	−.104	*−.381*	−.169	.145	−.042		*−.307*
Mean weight of seeds	−.165	*−.232*	*−.220*	−.205	.191	.147	.073	−.206	−.049	*−.307*	

Data from other progenies bearing on the relation of crossing over and the size of ear are rather meager, but the evidence is sufficient to indicate definitely that the relations shown in the larger progeny are not general. (Table 37.) Thus 17 reciprocals in Dh 416, Lanham, 1924, show a negative correlation of -0.47 ± 0.13 between crossovers in the male and the number of seeds on the homozygous parent, and that between crossing over in the ovules and the number of seeds on the heterozygous parent is positive, 0.34 ± 0.15. The data from the entire population substantiate the relation between crossing over in the ovules and the number of seeds, but the correlation between crossing over in the male and the number of seeds on the heterozygous parent, while negative, is insignificant, indicating that the restricted population of reciprocals was a chance deviation. Few of the coefficients in other progenies are significant, but the numbers are too small to detect correlations of the indicated magnitude.

TABLE 37.—*Correlations showing the association of percentage of crossing over with number of seeds*

Progeny	Characters correlated	Number of ears	Product moment coefficient of correlation(r)
Dh 416:			
L3L1C5L4L1L24, reciprocals.	Crossing over in ovules and number of seeds in heterozygous parent.	17	0.338±0.15
Do	Crossing over in ovules and number of seeds in homozygous parent.	17	.371± .15
Do	Crossing over in pollen and number of seeds in heterozygous parent.	17	−.012± .17
Do	Crossing over in pollen and number of seeds in homozygous parent.	17	−.472± .13
Do	Crossing over in pollen and crossing over in ovules	17	−.186± .16
Do	Number of seeds in heterozygous parent and number of seeds in homozygous parent.	17	.582± .11
L3L1C5L4L1L24, all ears.	Crossing over in ovules and number of seeds in heterozygous parent.	52	.332± .08
Do	Crossing over in pollen and number of seeds in homozygous parent.	55	−.126± .09
L3L1C5L4L23, all ears	Crossing over in ovules and number of seeds in heterozygous parent.	17	−.054± .17
Do	Crossing over in pollen and number of seeds in homozygous parent.	37	.030± .11
Dh 417:			
L1L2L1L2L23, all ears	Crossing over in ovules and number of seeds in heterozygous parent.	21	.208± .14
Do	Crossing over in pollen and number of seeds in homozygous parent.	19	.091± .16
Emerson and Hutchison (6):			
B–Lg, reciprocals	Crossing over in ovules and number of seeds in heterozygous parent.	19	.194± .16
Do	Crossing over in ovules and number of seeds in homozygous parent.	19	−.459± .13
Do	Crossing over in pollen and number of seeds in heterozygous parent.	19	−.199± .16
Do	Crossing over in pollen and number of seeds in homozygous parent.	19	−.337± .14
Do	Crossing over in pollen and crossing over in ovules	19	.262± .15
Do	Number of seeds in heterozygous parent and number of seeds in homozygous parent.	19	.012± .16
C–Sh, reciprocals	Crossing over in ovules and number of seeds in heterozygous parent.	20	−.129± .15
Do	Crossing over in ovules and number of seeds in homozygous parent.	20	.041± .15
Do	Crossing over in pollen and number of seeds in heterozygous parent.	20	−.091± .15
Do	Crossing over in pollen and number of seeds in homozygous parent.	20	.568± .10
Do	Crossing over in pollen and crossing over in ovules	20	.168± .15
Do	Number of seeds in heterozygous parent and number of seeds in homozygous parent.	20	−.206± .14

DISCUSSION

Cytological examination shows that the reduction divisions, in the strains of maize under consideration, occur approximately three weeks before the flowers mature. The period over which these divisions take place, though not well delimited, is about four days. Any factors which affect the proportion of crossover to noncrossover gametes subsequent to the reduction division would of necessity operate to bring about a differential death rate either of gametes or of zygotes.

If the actual rate of crossing over is susceptible to alteration through the influence of environmental factors, such factors must be operative three or four weeks before anthesis. Further, if the actual rate of crossing over can be affected only at the time of the reduction division, the period during which environmental factors can operate effectually is limited to a period of three to five days.

The method of measuring crossing over does not permit the separation of causes operative on the actual rate of crossing over from those affecting the gametic and zygotic proportions subsequent to the reduction divisions.

The field can be narrowed somewhat by measuring the gametic proportions at different periods, on separate inflorescences and on different parts of the same inflorescence.

A check on gametic death rates can be had by subjecting the gametes to adverse conditions, or death rates can be measured indirectly through correlating the apparent crossover rate with fertility.

With changes in the apparent rate of crossing over so small as those here considered, it is impossible to distinguish with certainty gametic changes from differential death rates of zygotic classes. To compare coupling and repulsion ratios the comparison necessarily is made between different progenies, and it has been shown that even closely related progenies may have different rates of crossing over.

It is apparent from the data considered in this bulletin that many factors, both environmental and genetic, affect the crossover rate. The results obtained with male and female gametes, with first and second ears, with homozygous and heterozygous *R*, and with butts and tips leave no room for doubt that each of these factors has a slight though significant effect upon crossing over. On the other hand such factors as vitality of the pollen, length of silks, and age of plants seem to bear no relation to the crossover rate, though in these cases the populations were not large enough to establish definitely their lack of effect within 3 or 4 per cent. However, for all these cases it seems reasonable to conclude that the factors considered are of minor importance, at most causing a difference of but 2 or 3 per cent and thus failing to provide an explanation for the occasional large nonheritable variations from the mean rate. The explanation for these variations must be looked for earlier in the ontogeny of the plant.

It is not inconceivable that environmental conditions of any two adjacent plants might differ sufficiently at the critical period when reduction and segregation divisions were in progress to cause the observed differences in the percentage of crossing over. Such factors, being no longer operative by the time the flowers had matured, could not be associated with the effects which they might produce.

As the work has progressed it has become increasingly evident that the distinction between factors that produce a measurable effect and those that do not depends not a little on the numbers involved in the several experiments. In other words, there appears to be a positive correlation between the degree of certainty assigned to the influence of a factor and the number of individuals involved in the experiment. Like other biological phenomena, crossing over appears to be not a thing apart but to react in a complex manner and in a varying degree to practically all changes in environment. There can be little doubt that, if more refined tests were made, many of the factors dismissed as producing no significant changes in the rate of crossing over would have to be transferred to the list of significant factors.

The present study seems to have eliminated most of the natural factors that could affect the gametic proportions subsequent to the

reduction division, and it is left for future investigations to determine the effect on crossing over of factors operative at an earlier period in ontogeny.

Finally, it is apparent from these studies that the percentage of crossing over, that is the degree of association of parental characteristics, is variable and can be altered by numerous factors, a condition which facilitates the dissolution of character combinations and permits flexibility in breeding.

SUMMARY

A comparison of the variability of the linkage between *C* and *Wx*, genes for aleurone color and endosperm texture, with that for other linked genes in maize shows that the *C*–*Wx* linkage is no more unstable than that for other linked pairs.

The variability of the crossover ratio in some progenies is greater than that of the ratios of the Mendelian characters involved, but this is not invariably so.

Crossing over between linked genes is not always more variable than the proportion of independent genes, indicating that the variability is not associated completely with linkage.

In a study of several progenies it is apparent that some are much more uniform with respect to the rate of crossing over than others.

A comparison of the variability in male as opposed to female gametes in 13 progenies shows that the rate of crossing over is as variable in one sex as in the other.

A comparison of the variability in upper and lower ears for three progenies shows that the rate of crossing over is equally variable in both ears.

The variability of the rate of crossing over was measured separately in the bases and tips of the ears of two progenies and was found to be alike for both sections.

The variability of the rate of crossing over in several samples of single individuals was found to be less than that in single samples of several individuals.

In 13 cases where pollen was divided into two lots, one being applied at once and the other being held for seven hours, the variability of the crossover ratio in the fresh pollen was as great as that in the old.

In seven cases where two samples of pollen from the same plant were used, one lot representing the first pollen shed and the other taken several days later, it was found that the pollen produced at the later date was no more variable with respect to the crossover percentage than that produced early.

A comparison of the observed variability of the crossover rate with that expected from the operation of chance factors, as calculated by $\sqrt{pq/H}$, shows clearly that the rate of crossing over in some progenies is no more variable than is to be expected, though in most cases it seems certain that factors other than chance are affecting the rate. In a series of 17 progenies the observed variability exceeds the expected ($\sigma_{50}-\sqrt{pq/H}$) by 3.53 ± 0.19.

From the results obtained with 17 related progenies it is clear that progenies differ widely in the closeness of the linkage between the genes *C* and *Wx*.

The behavior of a number of progenies for several generations shows that the rate of crossing over is often inherited, but this is not invariably true; and it seems necessary to conclude that occasionally environmental factors profoundly modify the rate.

A separation of the plants into those in which the aleurone factor *R* is homozygous from those in which this factor is heterozygous discloses the fact that plants heterozygous for *R* have a lower rate of crossing over than those homozygous for *R*.

A comparison of the rate of crossing over in plants heterozygous for the sweet endosperm factor *Su* with the rate of crossing over in plants homozygous for *Su* indicates that this factor may be associated with the crossover rate.

Plant reciprocals in 13 progenies show that the rate of crossing over is not alike in the two sexes. In some progenies the rate is higher in the male and in others in the female.

Crosses providing four classes of seeds but no linkage indicate that the proportion of the several seed classes is not alike in the reciprocals.

Pollen stored for seven hours produces a much higher proportion of waxy seeds than the fresh pollen. Although stored pollen produces waxy seeds in excess of equality, fresh pollen produces a significant deficiency of waxy seeds. On the other hand, the crossover percentage is not altered as a result of storing pollen, even though the viability of the pollen is reduced by about one-third.

Pollen produced early in the ontogeny of the plant has the same gametic proportions as that produced late.

From a consideration of the rate of crossing over on ears varying in length of silk, it seems clear that the length of silk is not an important factor in the survival value of the several gametic classes.

In three progenies the crossover rate was not alike in upper and lower ears when the female parent was homozygous recessive. In two of these progenies the rate was higher on the lower ears and in the other the rate was higher on the upper ears.

Ears in which the upper and lower halves were classified separately show a higher rate of crossing over in the tip than in the base, but this difference is found only when the female parent is heterozygous.

In some progenies crossing over in the male is found to be correlated with the number of seeds resulting from the use of this heterozygous pollen on homozygous recessive plants, but this is not true for all progenies. Such a correlation indicates a lower survival value for the crossover gametes of the male. Measures of vigor other than number of seeds were not found to be correlated with the crossover rate, indicating that the condition of the plant has no effect on the frequency of crossing over.

The distinction between factors that produce a measurable effect and those that do not depends in no small measure on the number involved in the experiments. With the factors here considered, the sizes of the populations varied widely in the several experiments, and there can be little doubt that if more refined tests were made many of the factors dismissed as being without effect would be found to change the crossover rate a small though significant amount.

None of the factors considered provide an explanation of the occasional wide departure from the mean crossover rate.

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